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A POPULATION STUDY OF THE TASMANIAN "COMMERCIAL" SCALLOP, *NOTOVOLA MERIDIONALIS* (TATE) (LAMELLIBRANCHIATA, PECTINIDAE)

By THE LATE W. S. FAIRBRIDGE*

(*Manuscript received May 22, 1952*)

Summary

The "commercial" scallop supports a dredge fishery in the D'Entrecasteaux Channel, Tasmania. There is probably a genetically homogeneous population in this area, and the juveniles possibly move from bed to bed, but the adult scallops form discrete, stable communities.

The statistical history of the fishery reveals a marked decline in the availability of scallops since some time between 1941 and 1945. A more exact statement cannot be made because fishing efforts in war time were not comparable in efficiency with those made before and since. Furthermore, before 1941 a second species of scallop was also fished, but not distinguished in the catch records.

The rings in the shell are formed annually and can thus be used for age determination. This can be demonstrated directly in young scallops by comparing the growth at the edge of the shell at successive seasons of the year. In older scallops the growth increments are too small to compare in the same way; the evidence of the annual character of the rings is here mainly indirect, although in its totality convincing. There is distinct variation in growth rate between different beds, and apparent variation between different age-groups from the same bed.

The age and size composition of the stocks were studied from samples taken from several representative beds from 1944 to 1949. The age composition studies showed that the year-classes produced in the period extending approximately from 1939 to 1941 predominated, and that very little recruitment had occurred since that period; the results of the size composition studies confirmed this. Scallop fishermen agreed that small scallops had been unusually scarce in the Channel for many years.

It is concluded that the scallop population is suffering primarily from a severe long-term shortage of recruits, the cause of which, although apparently natural, is unknown; and secondarily from overfishing, as the fishermen exhaust, one after another, the aging, isolated subpopulations of adults on the different beds. Unless ample numbers of recruits soon reappear, the fishery may come to an end.

(Since Mr. Fairbridge wrote this paper some beds of juvenile scallops have been located. Although the beds are not large, their presence indicates that the Channel population is still reproducing and that there could be a return to years of good recruit broods.)

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[*] A draft paper on the "commercial" scallop was completed by Mr. Fairbridge shortly before his death in May 1950. His manuscript was edited by two of his colleagues of the Division of Fisheries, C.S.I.R.O., who had also worked on scallop problems, and the present paper is the result. No important changes have been made.

I. Introduction

Three species of scallop are found in the D'Entrecasteaux Channel, the main area of the Tasmanian scallop fishery: the queen scallop, *Equichlamys bifrons* (Lamarck); the doughboy scallop, *Mimachlamys asperrimus* (Lamarck); and the "commercial" scallop, *Notovola meridionalis* (Tate). Only the last two have been fished for profit. The last is the principal species fished today, although the doughboy has been the main trade species at times in the past. This paper mainly concerns the "commercial" scallop, and references to the "scallop" refer to that species unless otherwise stated.

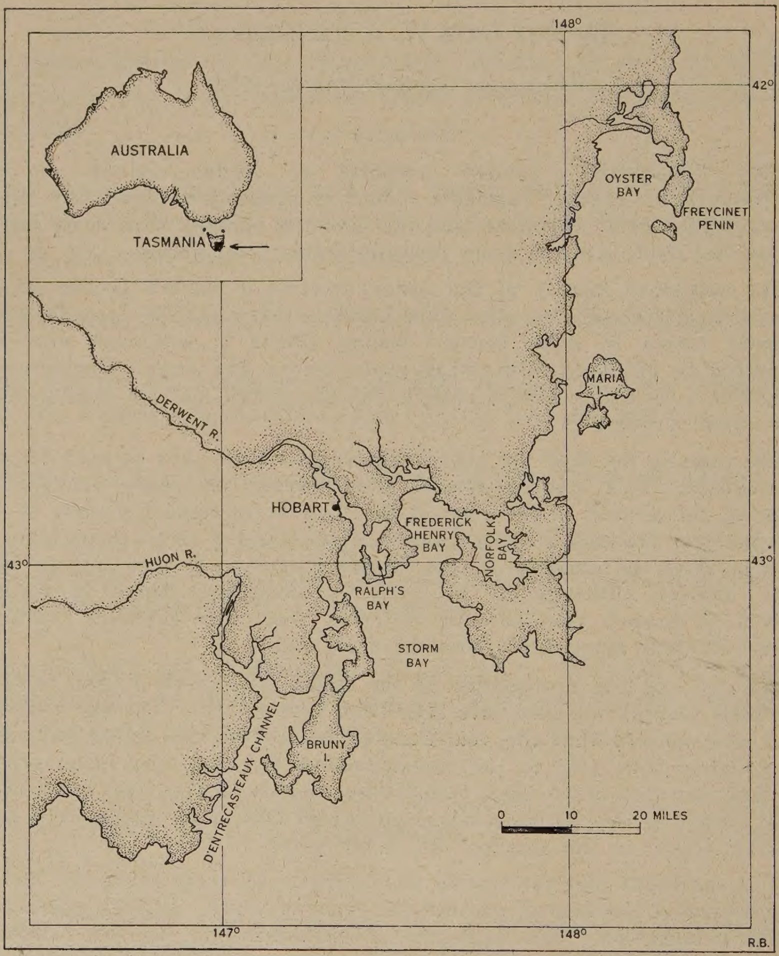
148°
42°
AUSTRALIA
TASMANIA
OYSTER BAY
FREYCINET PENIN
MARIA I.
DERWENT R.
HOBART
FREDERICK HENRY BAY
NORFOLK BAY
43°
HUON R.
43°
RALPH'S BAY
STORM BAY
BRUNY I.
D'ENTRECASTEAUX CHANNEL
0 10 20 MILES
147°
148°
R.B.

Fig. 1.—South-eastern Tasmania, showing D'Entrecasteaux Channel and other localities mentioned in text.

During the second world war the scallop fishing fleet doubled in size, and it was feared that many beds were being fished out. In 1944 the

Division of Fisheries, C.S.I.R.O., began an investigation. This paper deals with the history of the fishery, the age of the scallops on the different beds, and the condition of the stock.

Other grounds where scallops have been taken in Tasmania are Frederick Henry Bay, and Oyster Bay, west of the Freycinet Peninsula (Fig. 1). In both localities the water is oceanic. The species taken is the "commercial" scallop. It is known that scallops occur in large quantities (or have done so) off Flinders Island (Bass Strait) and Lakes Entrance (Vic.), and in Port Phillip Bay (Vic.). The species in Port Phillip Bay is *Notovola alba* (Tate) and another species, *N. fumatus* (Reeve), occurs in New South Wales waters, both very closely related to the Tasmanian "commercial" scallop. It is probable that the scallops taken in Bass Strait belong to one of these two species. Reports have been received from time to time of the capture of large numbers of scallops off the New South Wales coast. These reports come from Danish-seine net fishermen working in about 30 fathoms of water, in the area from Twofold Bay to Green Cape. Though their ordinary fishing results have recently been poor, none of these fishermen has turned to scalloping.

The Western Australian relative of the commercial scallop is *N. preissiana* Iredale (*bifidus* auct.). This occurs in the Albany area, but no large concentrations have yet been reported.

II. THE ENVIRONMENT

The D'Entrecasteaux Channel (Figs. 1 and 2) is about 25 miles long and in places only a few miles wide. Scallop fishing is limited to within the 10-fathom line, and is carried on mostly in 7-8 fathoms. Such depths are common in the northern part of the Channel. The southern part is deeper and little fished, and probably does not carry many scallops. The bottom is of broken shell and fine to coarse sand, and, in places, mud. Scallops are found in commercial quantities on all types of bottom. Two moderately large rivers, the Derwent and the Huon, reach the sea in the region of the northern and southern ends of the scallop grounds respectively. Hydrological sampling has shown that neither river has much effect on the northern half of the Channel, where the salinity of the water is virtually oceanic. Only during occasional flooding of the Huon River is the salinity of the surface water depressed, while even then the bottom water is only slightly affected. Temperatures vary from 7 to 20°C.

Plankton hauls on which these observations are based were made at six stations on the scallop beds, at monthly intervals over 2 years. Monthly intervals are rather too large for tracing seasonal changes in plankton abundance; but a certain regularity is observable in the occurrence of heaviest diatom and dinoflagellate populations from about September to November (i.e. spring), followed by heavy zooplankton catches in early summer; zooplankton catches at other times being poor.

The diatoms and dinoflagellates are present more often than not, and often in extremely large numbers. This is in marked contrast to hauls made within similar nets at the 25-30 fathom line on the east coast of Tasmania.

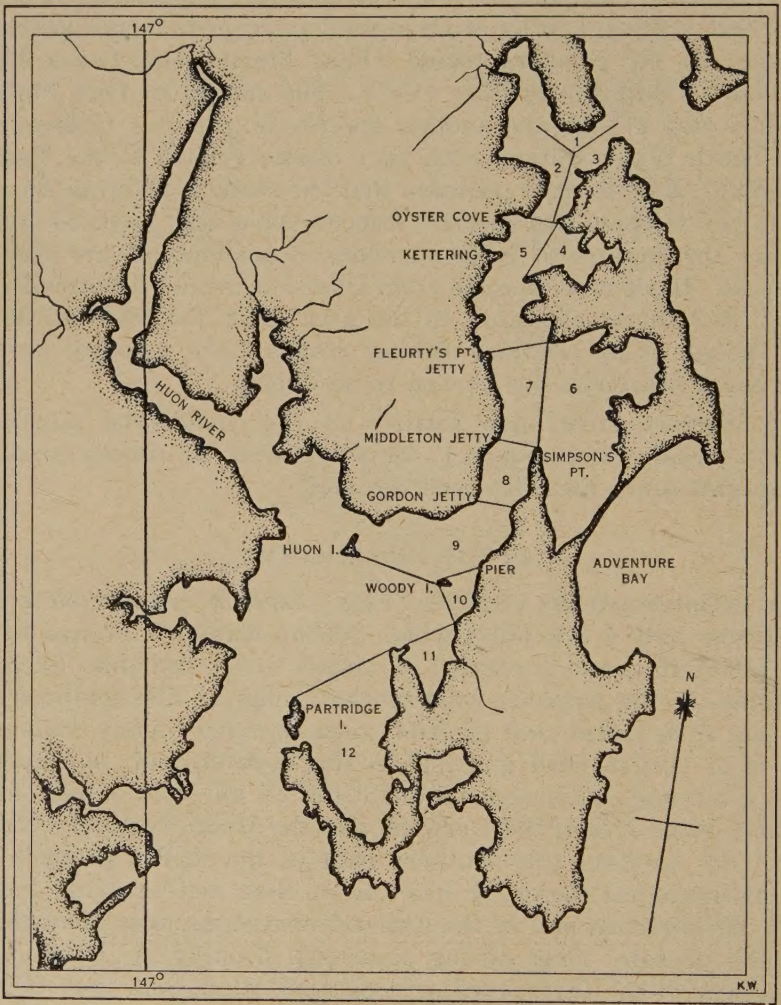
147°
1
2
3
OYSTER COVE
KETTERING
5
4
FLEURTY'S PT. JETTY
7
6
HUON RIVER
MIDDLETON JETTY
SIMPSON'S PT.
8
GORDON JETTY
HUON I.
9
PIER
ADVENTURE BAY
WOODY I.
10
11
N
PARTRIDGE I.
12
147°
K.W.

Fig. 2.—D'Entrecasteaux Channel, showing localities and numbered areas mentioned in text.

Table 1, supplied by the Hydrology Section of the Division of Fisheries, gives mean phosphate phosphorus values of water samples taken at Tinderbox and Gordon, i.e. at the northern and southern end respectively of the main scalloping area of the Channel (areas 1 and 9 in Fig. 2).

The rate of turnover of the nutrients is presumably high, in view of the persistent diatom flowerings. Table 1 shows that there is no complete exhaustion of the phosphates at any time of the year, as there is in some Australian estuaries. Phosphate concentrations are high on the average, and never fall very low.

TABLE 1

MEAN PHOSPHATE PHOSPHORUS VALUES (μg. P/l.) FOR TWO STATIONS IN THE D'ENTRECASTEAUX CHANNEL

		Gordon			Tinderbox		
		Inorganic	Organic	Surface Inorganic Minimum	Inorganic	Organic	Surface Inorganic Minimum
Winter, May-Sept. 1947	Surface	5	11	1	6	12	1
	Bottom	4	11		6	21	
	No. of Readings	(5)	(4)		(5)	(4)	
Summer, Oct. 1947-Apr. 1948	Surface	9	8	4	6	9	2
	Bottom	9	10		9	8	
	No. of Readings	(7)	(6)		(7)	(6)	
Winter, May-Sept. 1948	Surface	10	3	6	11	6	1
	Bottom	10	7		10	5	
	No. of Readings	(5)	(5)		(5)	(5)	
Summer, Oct. 1948-Apr. 1949	Surface	5	10	0	6	6	4
	Bottom	6	8		6	8	
	No. of Readings	(7)	(6)		(7)	(7)	
Winter, May-Sept. 1949	Surface	9	5	7	9	6	6
	Bottom	9	3		9	8	
	No. of Readings	(5)	(5)		(5)	(5)	

The nutrient wealth is no doubt due to heavy run-off from the adjacent land, as well as from the two rivers; and it is noteworthy that the area is circumscribed and shallow, and subject to strong tidal currents which effectively mix the water. The currents enter and leave by both ends of the Channel, so that the identity of the Channel water mass is maintained, and any change would be gradual. There is some evidence that swift tidal currents are favourable to scallop growth (e.g. in areas 1, 9, and 10) ; but the point is difficult to prove, because the best beds have been the most heavily fished and tend today to be depleted and poor.

In contrast to the rich phytoplankton population, the zooplankton is poor. Small copepods predominate, with Cladocera often occurring and crab larvae occasionally swarming. Open-sea forms such as *Calanus* are found in the deeper, southern part of the Channel, and euphausians often swarm there in the warmer months, but in the shallower portion such forms are only stragglers. Occasionally estuarine species, such as the copepod *Gladioferens,* occur; but these also are apparently only stragglers.

The diatoms are important as a direct source of food to the scallop. Scallop stomachs are often packed with them, some being larger than

0.5 mm. in diameter and still united in chains of four or five individuals. Phytoflagellates are also common in the stomachs, as are various algal and other plant materials. The scallop is evidently able to reject most of the inedible grit etc. in the water.

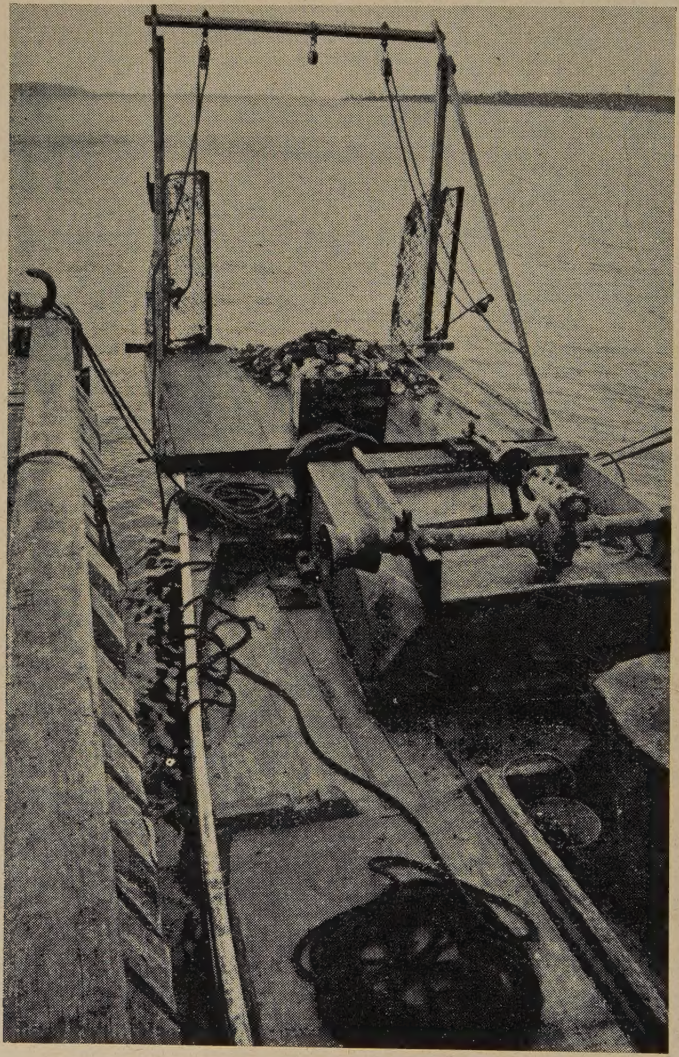

Fig. 3.—Dredging arrangements on a Tasmanian scallop boat.

Scallop fishing was once carried on in the Derwent River estuary from just above the present Hobart bridge southward, and in Ralph's Bay. Here again the salinity is virtually oceanic, but floods are liable to occur.

III. The Fishery

Scallops are caught in Tasmania by dredging. In the past the usual type of vessel has been the ordinary engine-powered Tasmanian fishing sloop or cutter, with a crew of from one to four (usually two) men. Each boat works one, two, or three dredges. Dredges were formerly hauled by hand, but most of the boats had changed over to power-driven winches by 1943. A platform and gallows is usually erected, overhanging the stern of the craft, to give working room and overhead sheaves for the dredge warps (Fig. 3). In bad weather, when the dredges tend to "lift" off the bottom, the scallopers always seek sheltered grounds. Recently, a larger type of boat, 40-50 ft. long and powered with a heavy diesel engine, has been entering the scallop fishery. These boats were working up to six dredges until 1949, when all boats were limited to two.

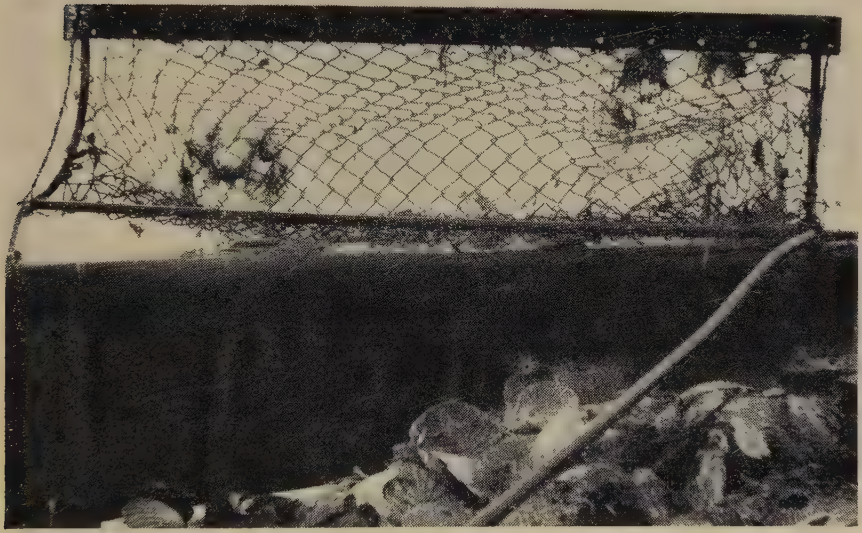

Fig. 4.—Tasmanian scallop dredge and portion of catch.

The dredge used has a mouth about 1 ft. high and the width of 4 ft. is a maximum fixed by regulation. The bag is about 2 ft. deep and is of "Cyclone" wire netting which remains stiffly open when the dredge is working, and should not collapse and fall shut (Fig. 4). Shells 2 in. and less in length readily escape through the meshes, and are only retained as a result of clogging. The dredge usually takes much detritus, amongst which occasional juvenile scallops down to 1 cm. long may be found; but the proportion of such shells being lost is still conjectural. It is noticeable that, if small-meshed wire netting is used inside the bag of a dredge, more small scallops may be brought up.

The lower bar of the dredge mouth is a flat blade set at an angle and skill is needed to put the correct "set" on this blade. This depends upon length of rope or wire, the depth of water, hardness of bottom, speed of the current, and the speed of the vessel (usually about 3 knots). The bottom is usually worked in narrow "strips" of a few hundred yards to a mile in length, the boats towing alternately with and against the current; very occasionally they work across the tide.

At the start of the season the boats scatter, looking for the best ground. But very soon they congregate where they see the best hauls being made, and often 10-12 boats may be seen working a very confined "strip" for a day or more. It is often considered advantageous to dredge immediately behind another boat. The dredges are usually hauled at the end of each run down the "strip", but they may be emptied more often. A dredge quickly fills up where there is much detritus or where scallops are thick. It is said by the fishermen that a "strip" needs to be dredged for an hour or more before it will yield good catches. This observation is so often repeated that it must be believed.

When the dredge is hauled up it is emptied and immediately lowered again. The scallops are culled from the rubbish and stored in sacks on deck, where they may be kept for one or two days. On sunny days the sacks are kept wet with sea-water, but it has been found that rain very quickly kills a scallop. Unlike the oyster, the scallop cannot retain water inside the closed shell; storage is therefore much more difficult for the fishermen, and the scallops are usually cleaned the day of capture or the day after.

The cleaning consists of cutting the adductor muscle (the "eye") away from either valve and from the stomach. The muscle is retained together with the attached hermaphrodite gonad, and the shell, mantle, and viscera are discarded. A regulation made in 1926, and enforced since 1932, prohibits cleaning the catch at sea during fishing. The regulation was made in the belief that the throwing of scallop waste on the beds encouraged starfish.

The cleaned scallops are washed and stored in tins with perforated bottoms for draining. Since the scallop season is confined to the cold months, the matter of preservation is not paramount. The scallop meats may be sold fresh in Tasmania, or canned there, or exported in the frozen state to the Australian mainland. In recent years some have been sent to the United States of America.

IV. The History of the Fishery

Scallops seem to have been overlooked by the Tasmanian public until the first decade of the twentieth century. In a Royal Commission Report on fisheries in 1882 "*Pecten* spp." are mentioned last of a number of edible shellfish. Another Royal Commission in 1916 does not even mention scallops.

However, the Tasmanian Commissioners of Fisheries in their Reports for 1917-18 and 1918-19 include special reports on the scallop beds in the Derwent estuary close to Hobart (Flynn 1918, 1919). These reports state that beds in the upper Derwent (i.e. above the present Hobart bridge) that had once been productive were wiped out as a result of floods in the last week of 1916, but that in 1919-20 the Derwent was "alive" with young scallops (Fig. 1).

After the first world war a definite scallop fishery began to develop. The following history of it has been compiled from several sources: (i) reports, which include data on annual catches and efforts, published successively by the Commissioners of Fisheries, the Sea Fisheries Board, and the Tasmanian Department of Agriculture; (ii) verbal and written statements made by the Tasmanian Inspector of Fisheries and by fishermen; and (iii) personal observations made by the writer and his colleagues, mainly since 1944.

Before 1918, the scallop beds in the Derwent were fished casually by amateurs in the week-ends, working mostly with small dredges from rowing boats. Both commercial and doughboy scallops were caught.

From 1919 scallops were being taken for sale. Figures are available for the numbers sold in the fishmarket in 1922 and 1923, but these would not include the greater part, which was sold direct to hotels. No other records for this period are available. In 1920 there were not more than two boats working commercially, in 1923 two or three others entered the trade, and in 1924 many others.

During this time (i.e. 1919-24) the fishery gradually shifted downstream from the small beds in the immediate vicinity of Hobart towards the mouth of the Derwent (Fig. 1) and into Ralph's Bay (for doughboys); while another fishery, the present one, sprang up in the northern half of the D'Entrecasteaux Channel (for commercials). Scallops had been known to occur in the Channel for many years before they began to be exploited. Opinion is divided as to the reason for the shift by the fishery from the beds around Hobart.

Flynn (1918) suggests four possible causes for a sudden dearth of scallops (doughboys and commercials) on the Hobart beds:

(1) Reduction of salinity, due to floods;
(2) Silt brought down by floods, either smothering the scallops or promoting the growth of the worm *Polydora;*
(3) Predation by starfish or crabs; and
(4) Parasitic protozoa.

Later Flynn (1919) found the Derwent again stocked with young scallops (commercials) and concluded that their previous disappearance had been caused by unusual flooding, acting either by (1) or (2) above.

Suggested reasons for the subsequent virtual extinction of doughboys and commercials in the Derwent are overfishing, pollution by factory effluents, or excessive silt brought down as a result of increasing land usage and soil erosion. However, there is little definite information. It is unlikely that fresh water would directly act on the scallops even during flood; during a flood the bottom salinity (4 fathoms) at Hobart was 32.87 parts per thousand, while the surface salinity was 5.1 parts per thousand (E. R. Guiler, personal communication). Flynn (1918) states that very few of the dead scallop shells of the upper Derwent did not show the effects of infestation by *Polydora,* whereas the disease was "practically non-existent" among the scallops off Gordon (D'Entrecasteaux Channel). Today, when the scallops are on the wane in the Channel, the infestation by *Polydora* seems to have increased there.

It seems likely that the scallop beds in the Derwent were never very stable. An estuarine environment is certainly unusual for Tasmanian scallops today, although a few are taken in the entrance to the Huon River.

In 1925 restrictive legislation virtually ended commercial scalloping in the Derwent estuary (including Ralph's Bay).

In the same year the northern beds of the D'Entrecasteaux Channel (areas 1, 2, and 3 in Fig. 2) were closed to scalloping, evidently from fear of overfishing. There must therefore have been considerable previous fishing in this area. These beds were subsequently opened to fishing, closed again in 1930 and 1931, and afterwards reopened. Since 1925, scalloping has been virtually confined to the Channel.

From 1929 onwards, total catch figures (in thousands of scallops) are available in the Reports of the Sea Fisheries Board and Reports and unpublished papers of the Department of Agriculture. These figures were at first collected verbally from fishermen and buyers by the Inspector of Fisheries. In 1941 a system of obtaining written statements (returns) of catch from fishermen was inaugurated, and this was improved in 1943. Checks made with the scallop buyers indicated that these returns were reliable. In 1947 a special return system was introduced for scallopers: the Channel was divided into 12 areas (Fig. 2), corresponding roughly with the established scallop beds, and the scallopers were required to make weekly returns stating the weights of cleaned scallops obtained from each locality. In Table 2 and Figure 5 these weights have been converted on the basis of 40 lb. per thousand cleaned meats (adductor muscle and gonads).

The open season for scallops was fixed, in 1924, from May to August inclusive. These are the months when the scallop is in best condition. It later became evident that in some years the scallops began spawning in August, and the gonads of scallops taken at this time sometimes burst, after cleaning, in the packed containers. Accordingly the season was reduced by 2 weeks (ending on August 15) in 1940, 1941, and 1942, and again (after it had been restored to its original length for 3 years, as a war-time measure to obtain a greater yield) from 1946 onwards. In Table 2 and Figure 5 the mean catch per dredge figures for those years have been raised by one-seventh, to make them comparable with the other figures, which are on a 4-month season basis.

The legal minimum size for the doughboy scallop since 1925 has been $2\frac{3}{4}$ in. in its smallest diameter. The legal minimum for the "commercial" scallop was $3\frac{1}{2}$ in. in its widest diameter until 1935, and $3\frac{1}{2}$ in. in its smallest diameter since that date. In 1935 the width of dredges was limited to 4 ft. In 1949 a limit of two dredges per boat was imposed.

TABLE 2

CATCH, FISHING EFFORT, AND MEAN CATCH PER UNIT EFFORT OF TASMANIAN SCALLOPS IN THE YEARS STATED

Catches can be converted to weight of scallop meats at 40 lb. per thousand. The 1948 figures do not include certain catches made in Norfolk Bay, i.e. outside the Channel. For further explanation see text

Year	Licensed Vessels	Licensed Dredges	Total Catch (thousands of scallops)	Catch per Dredge (thousands of scallops)
1922			3,354	
1923			4,183	
1929			4,500	
1930			5,400	
1931			4,030	
1932			6,280	
1933	15	30	8,457	281.9
1934	21	35	10,000	285.7
1935	20	34	11,753	356.2
1936	22	38	12,872	338.7
1937	20	36	14,186	383.4
1938	26	50	18,000	367.3
1939	27	52	17,200	330.8
1940	20	43	14,000	372.1
1941	27	54	18,600	393.6
1942	26	51	11,149	249.8
1943	32	63	12,280	194.9
1944	46	90	14,120	156.9
1945	48	98	16,463	168.0
1946	54	122	21,480	201.2
1947	51	118	23,872	231.2
1948	50	118	20,595	199.4
1949	35	70	12,951	211.5
1950	36	72	11,260	178.7
1951	41	82	9,013	125.6

Figure 5 has been constructed from the historical and statistical data of Table 2. The lowest line shows the number of boats licensed in each year for scalloping. The top line shows the annual catch of scallops in millions.

A small licence fee is paid for each scallop dredge. The number of dredges licensed in each year since 1933 is given in the above-mentioned Reports. The catch of a boat is dependent almost directly on the number of dredges used, and the dredge is therefore a convenient unit of fishing effort. The middle line in Figure 5 represents the catch divided by the number of licensed dredges, for each year, and illustrates the changes in the catch per unit fishing effort. This is the most direct measure of the availability of scallops. The inspection of the area is thorough, and evasion of dredge licensing is negligible.

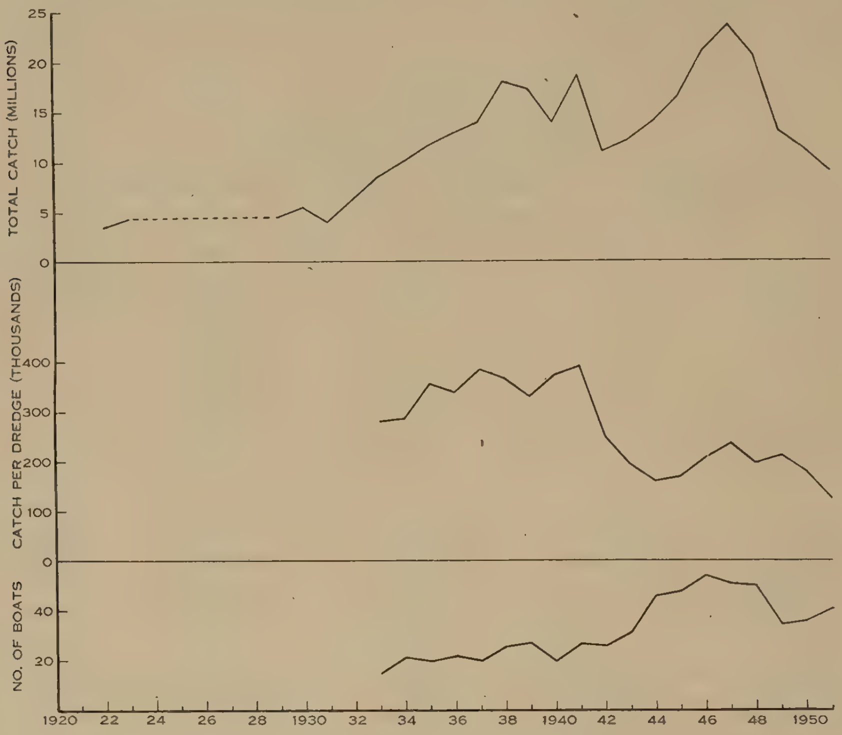

Fig. 5.—History of the Tasmanian scallop fishery: total catch, mean catch per dredge, and number of boats fishing, in each year for which records are available. Catches are in numbers of scallops. For further explanation see text.

Figure 5 shows that, after the exploratory period of the 1920's, about which there is no good statistical information, there was a gradual increase in the annual total catch and mean catch per dredge. After 1941 they both fell, although the fleet was growing in size. The increased fishing effort gradually restored the total catch to about its former maximum by 1945, but the catch per dredge was by then less than half of its recorded maximum.

These changes, from 1942 to 1945 inclusive, were all at least partly due to the war. The efficiency of the scallopers was reduced because of petrol rationing, which made it difficult for them to move from ground to ground in their normal way, and because of lack of men to open the scallops, which meant that the fishermen had to spend a considerable time in port opening their own scallops, when they would otherwise have been fishing. These factors contributed to the decline in the catch per dredge and total catch, and some observers felt at the time that no other explanation was necessary. The increase in the number of scallop boats fishing per year, which eventually restored the total catch in spite of the fall in catch per unit effort, was due to the rather generous treatment afforded the Tasmanian fishing industry, and certain Tasmanian fisheries in particular, by the authorities administering manpower and other controls. The scallop fishery was held to be an efficient fishery and was encouraged, although not to the point of providing labour for opening the catch.

With the end of the war the manpower position eased and was normal by 1947 or 1948. The catch per dredge responded immediately, but the improvement was small and short-lived (Fig. 5). The catch per dredge in the post-war years did not approach that of before the war. The total catch rose to a maximum in 1947, declined slightly in 1948, and declined precipitately in 1949. The decline in 1949 is partly due to a regulation restricting boats to using not more than two dredges each. This reduced the number of dredges from 118 in 1948 to 70 in 1949. But even so, the catch per dredge did not recover even to the 1947 level.*

Undoubtedly, therefore, there has been a serious reduction in the availability of scallops since before the second world war. The point at which this reduction should have been first detected in the level of the catch per dredge was obscured by the effects of the war. It must have occurred between 1941 and 1945, but over this period the catch per dredge was not comparable with the catches before or since. Taken at their face value these results appear to be typical of an overfished stock.

However, there is a serious limitation to the data. The statistics quoted and graphed do not all refer to the same species of scallop. Both the doughboy and the commercial are involved; and these species may have quite different life histories, habits, and population reactions to fishing.

None of the Reports states specifically to which species of scallop the published catch figures refer. In order to piece together the order of events that have occurred, the author had to interrogate scallopers and others interested in the industry. Though the information is hearsay, the accounts agree very well. There are also various printed sources which give verification, and there can be no doubt of the broad conclusions.

As already mentioned, about the time of the first world war both doughboy and commercial scallops were being caught in the Derwent estuary. In the early days of scalloping in the Channel, the commercial scallop was taken, e.g. near Kettering in 1926. During the 1930's the Channel scallops were preponderantly doughboys; it seems that scallopers would market doughboys, commercials, or mixed, and different prices were charged for each category. The following are extracts from some typical reports of this period.

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* The 1950 and 1951 seasons revealed a further decline in the catch and catch per dredge. Mr. Fairbridge's Figure 5 has been amended to show this.

In Report of Tasmanian Sea Fisheries Board, 1930-32: "The varieties of scallop most common . . . are the Commercial and Doughboy, the latter, so far as present known beds are concerned, being by far the most plentiful."

In report from the Secretary, Sea Fisheries Board, April 1936: "Between 50 and 60 hauls were made (over the whole area from Woodbridge to Gordon) and in no instance did the dredge fail to collect scallops in quantity varying from 200 to 600 in a dredge. The variety predominating was the doughboy, while a fair sprinkling of the commercial was discovered. The scallops were 50 to 60 per cent. marketable size. . . . The tests confirmed . . . that there is a preponderance of commercial scallops on the eastern and western sides in the upper part of the Channel, while in midway channel and eastern bay waters the doughboy variety is much more numerous. . . . "

Letter from the Secretary, Sea Fisheries Board, July 1938: " . . . there appears to be no diminution in the quantity, particularly respecting the commercial. It is said that the doughboy up to 2¾ in. is not so plentiful, but there are large stocks . . . up to 2½ in. Dredging on the beds this year discloses the presence of high quantities of small scallops, both commercial and doughboy, ½ in. up to 1½ in. diameter."

But after 1940 few doughboys were marketed. This was initially due to increased abundance of the more valuable "commercial" scallop. The thereafter refer only to the commercial. When the author first visited the scallop beds in 1944 doughboys were being caught and discarded by the scallopers. Today doughboys are relatively rare though it is reported that they may be becoming more numerous.*

It seems that during the last 20 years the doughboy has become scarcer, and the commercial has become, until recently, more plentiful. Doughboy meats weigh about 18-20 lb. per thousand, and commercial meats about 38-42 lb. per thousand. Opening (which is always an important economic problem) therefore is far quicker with the commercials. Had there been beds of commercials as rich in the 1930's as there are today, or were a few years ago, there is no doubt the scallopers would have concentrated on these despite the good fishing for doughboys. In fact, however, all reports agree that in the landed catches the doughboys preponderated.

It is evident that, during about 30 years of scallop fishing in Tasmania, there have been some major fluctuations in the populations of the two species concerned. Thus the superficially typical course of events indicated by Figure 5 can by no means be taken entirely at its face value and further facts must be called upon. Furthermore, there might be more than one population of the commercial scallop.

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* They became more numerous in the 1950 and 1951 seasons, i.e. after Mr. Fairbridge wrote.

Some criticisms have been made of the reliability of the catch per dredge as a measure of abundance. The most serious objection is that a scalloper will often license three dredges, while never working more than two—the third, and sometimes even a fourth, being carried as a spare. Or he may use two dredges at certain periods and three dredges at other periods in the same season, having licensed the greater number for the whole season. For statistical purposes, the number of dredges has been taken as the number licensed. No other data are available for the years prior to 1947. The mean catches per dredge have therefore been understated in Figure 5. However, all that is required is a valid comparison between years. Since scallopers presumably have always carried spare dredges the figures for all the years should remain broadly comparable. In 1949 scallopers were limited to working two dredges per boat.

V. POPULATIONS OF THE COMMERCIAL SCALLOP

It is necessary to determine as a first step whether or not the Channel supports a single homogeneous population of commercial scallops.

Although the larva has not been identified and its planktonic distribution is unknown, it can be assumed that its mode of life resembles that of other Pectinidae (Gutsell 1930 and references there). That being so, the larvae originating from any one area in the Channel can hardly fail to be distributed throughout most, if not all, of the scallop-carrying parts of the Channel. Drift bottle experiments have shown that there is no greatly preponderating surface-water movement to north or south but that under the influence of the tides the water moves in and out of both ends of the Channel. A bottle released off Gordon may be carried to either end of the Channel within a few days. The scallop larvae would be entirely at the mercy of these movements. After a backward and forward movement within the Channel each survivor would, in the course of a few days or weeks, reach the stage of development where it would have to seek bottom or die. Those that happened to be over an area of suitable bottom, whether inside or outside the Channel, would have a chance of survival. The scattering of bottom-seeking scallop larvae within the Channel must therefore be virtually complete.

Spawning appears to be a gradual or intermittent process, extending over some months. Such a prolonged spawning would tend to reduce the chances of all the brood of one year encountering unfavourable conditions, and would ensure its wide distribution.

It can thus hardly be doubted that the scallops in the Channel are a genetically homogeneous population. The species is hermaphrodite, but cross-fertilization is probably the rule.

Localized differences in the scallop shells, presumably representing different environmental effects, can be detected in the samples from various parts of the Channel, and there are constant morphological differences between areas. From this it may be taken that, although the adult swims, it does not move in numbers from one area to another. There are, therefore, more or less clearly delimited subpopulations in the various bays and straits of the Channel which must be treated, for certain purposes, as entities.

The differences can be detected by eye, merely by handling samples from the different areas, and perhaps the most obvious is the nature of the epizootic growths on the flat valve. Others are the colour, shape (width to length), weight, brittleness, and markings (growth rings) of the shell.

Most epizootic growths are transitory and a scallop moving from one area to another would presumably lose some epizootes and acquire others. But this would not be true of all epizootes, especially of the calcareous tubes of serpulid worms. Scallop shells from area 2 (Fig. 2) are usually heavily encrusted with these tubes, while those from neighbouring localities are free.

Shell colour may also be transitory, but to what extent is not known. Shells from east of Simpson's Point are characterized by brownish coloration.

The growth rings will be dealt with more fully later. Here it need only be pointed out that the pattern of growth rings is often characteristic of an area or of a proportion of the shells from an area. Some beds have been sampled through 5 years and no dispersion of characteristically marked shells has been detected. Particular mention may be made of a series of shells with a relatively small l_1 and large l_2,* taken in numbers year after year in the vicinity of Gordon only. Age determination showed that these shells were all of the 1939 and 1940 year-classes. There is no characteristic growth pattern assignable to all the shells from a certain locality, since the year-group also has a marked effect on the growth pattern, but it is observable that particular patterns occur among samples from certain areas only.

Shell weights have been determined in samples from various areas, and it is believed that some areas carry characteristically light shells. Shell thickness, however, is probably associated more with age than with size (length). On account of this confusing factor no exact figures are given to illustrate the differences.

A linear relation of shell width to shell length was found in the commercial scallop. Regression equations were calculated for two sets of samples from six areas. The samples were taken in June 1945 and in March 1946. The relevant data are set out in Table 3. Values for t are those obtained for between years.

There are highly significant differences between areas in both the yearly sets of samples. For the sake of brevity these are not shown in Table 3. But it is shown in the right-hand column that there are also some differences (t greater than 1.96, the number of degrees of freedom for t in these tests being ∞) between the samples obtained from the same area on the two occasions. The explanation seems to be that the local differences in question are very local indeed, and that the differences in successive years resulted from slight changes in the locality of sampling (not noticed or not thought to be significant at the time) on the two occasions. The three localities where this occurred (Sheppards, Barnes Bay, and Gordon) were not so definitely marked off as were Apollo Bay and Simpson's Point, for which there were no significant differences between the two samplings.

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* See Table 4 for definition of l_1 and l_2.

TABLE 3

REGRESSION OF SHELL WIDTH ON SHELL LENGTH IN SCALLOPS COLLECTED IN TWO SUCCESSIVE YEARS IN THE STATED AREAS, REGRESSION COEFFICIENTS, AND t VALUES IN TESTS OF SIGNIFICANCE OF DIFFERENCE BETWEEN REGRESSION COEFFICIENTS

Area . . (see Fig. 2)		Regression Coefficient, b		Error of b		t
		1945	1946	1945	1946	
1	Tinderbox	1.2499	1.1338	0.044	0.043	1.89
2	Sheppards	1.1995	1.0065	0.025	0.047	3.63
4	Barnes Bay	1.2138	1.3073	0.032	0.033	2.03
5	Apollo Bay	1.1899	1.1590	0.031	0.039	0.62
6	Simpson's Point	1.1741	1.2009	0.023	0.034	0.65
9	Gordon	1.2595	1.1364	0.023	0.027	3.47

Further work might show how localized these subpopulations may be. For the present it is enough to know that such groups exist.

Finally it is shown later, from the length frequency graphs of samples taken through a period of over 2 years, that the size distribution of scallops differed between the various areas, and that the differences were broadly stable over the period of sampling.

It is clear that the local environment (and this may be very local) has a strong influence on the scallop in the course of its life, and that the adult scallop remains in the same area.

The above-mentioned findings refer to scallops of about 60 mm. and over, and about 5 years old and over. It is possible that the young, especially in the 0- and 1-group, are not so restricted. For lack of material it has not been possible to study any of the above characteristics in these age-groups. It is quite possible that the particular length-width relation of a certain locality might be assumed by an individual only after it had passed through the 0- and 1-group stages, and it is not to be inferred that concentrations of very young shelled scallops would not become scattered throughout the Channel. Underwater observation has shown that the young small scallops swim more than the larger ones, which are relatively heavier in proportion to their surface area. It is quite feasible that by swimming consistently on flood or ebb tides the very young scallops might achieve considerable unidirectional movement.

VI. Age Determination and Growth of the Commercial Scallop

(*a*) *Nature of the Growth Rings*

Most lamellibranch shells bear clearly marked rings occurring at more or less regular distances from the origin of growth. Numerous authors have called them age rings, assuming that they are formed by an annual cessation of growth. Some authors have tested this assumption and found it true of particular species in particular localities; e.g. Weymouth (1923) for *Tivela stultorum* Mawe. Other workers have found the assumption untrue, or unreliable; e.g. Coe and Fox (1942) for *Mytilus californianus* Conrad.

There are numerous references to growth rings in the Pectinidae, but little critical work has been done. Dakin (1909) mentions the presence of rings in the shells of *Pecten maximus* L. and *P. opercularis* L., and assumes them to be annual. Gutsell (1930) describes the formation of a ring in the shell of *P. irradians* Lamarck at the time of first spawning; however, as almost all the specimens of this species were being caught before second spawning, there was little chance to observe the formation of subsequent rings. Dalmon (1935), working on *Chlamys varia* L., describes a cycle of shell growth — emaciation — fattening — spawning, in winter and again in summer. This results in the formation of two rings in the shell each year; however, the ring formed during the summer period of emaciation is fainter than that formed in the winter period of emaciation and is liable to be worn off the shell. Stevenson (1934) describes the growth of *Placopecten grandis* Solander as studied from the rings in the shell, but does not describe any test of the method. Similarly, Tang (1941) calculates the growth of *Pecten maximus* L. from the rings, but suggests that there is only "probably a good deal of agreement" between the number of rings in the shell of a specimen and its age.

The formation of the lamellibranch shell ring is described by Coker *et al.* (1921). From observations on captive freshwater mussels they concluded that the heavily marked rings (in this case formed in winter) are formed by a prolonged period of intermittent deposition of periostracum and prismatic layer underneath the old edge of the shell. As winter approaches, and again as the water warms in spring, the mantle is presumably alternately extended and withdrawn under the influence of the warm and cool spells. During the continuing warmth of summer growth is steady and normal shell is laid down without interruption. If the mussels are disturbed, or meet unfavourable conditions during the period of steady growth, the mantle is withdrawn. When growth is resumed, a sharp line becomes apparent where growth has ceased. The clarity of this line is dependent on the degree of disturbance to the mussel, but it does not usually approach the clarity of the relatively wide band of repeatedly interrupted growth which is characteristic of the winter. Weymouth (1923) concludes that this is substantially the case also in the Pismo clam.

In the "commercial" scallop, the flat valve is the one most suited to the study of the growth rings. Measurements may be made from the umbo, ventrally towards the free margin. The upper surface of the flat valve is raised in minute concentric ridges, parallel with the growth rings, in dorsoventral section looking like teeth of a comb. These ridges have a definite structure, and probably correspond with the periostracum of other lamellibranchs (cf. Dakin 1909). They are regularly spaced, but become taller and closer together as the ventral edge of the shell is approached, until finally they obscure the markings on the shell. This material must be scraped away in order to see the rings, particularly around the edge of the shell where the rings are often very close together. There is no chance of scraping away the ring itself; the coloured prismatic layer underneath is very hard, and even when this is removed the sharp line of the break in growth is visible in the nacreous layer below.

By wetting the shells, the colours are darkened and the rings are easier to see. The first four or five rings are usually clearly marked (Plate 1, Fig. 1). The ring itself is white, even after prolonged scraping, and this contrasts with the rest of the upper surface of the shell which is yellow, brown, pink, or purplish.

The early rings in the flat valve do not show marked discontinuity of growth. In general, each one forms in a slight depression of the surface, while the ensuing growth forms as a very low arch and subsequent depression toward the next ring. The surface of the flat valve in this region in dorsoventral section therefore has the appearance of a series of regular, very shallow waves, the rings being in the troughs.

Towards the edge of old shells, growth is evidently much slower. Scraping is essential to reveal the rings here, as there is usually much white periostracal matter on the surface. Always there is a sharp difference in the level of new growth after a ring in this region. The shell thus takes on the form of a series of steps, descending from the direction of the hinge to the periphery, the descending face of each step corresponding to the ring. In a minority of instances the shell continues to be coloured in between the whitish rings. In the majority, however, growth between the rings is so slight that there is not room for the colour of the shell to show up clearly, save perhaps as a grey-blue. In this region, therefore, it is easiest to proceed by counting the steps. For all of these reasons it is hard to show the age of old shells in photographs.

Evidence of abrasion of the edge is frequent (Plate 1, Fig. 2). The clearest evidence is where one segment of the periphery has been worn or broken away, and not the rest. Abrasion may occur during the early life when the first four or five rings are laid down, but it is much more common later.

Counting the rings near the edges of old shells is difficult, and is liable to subjective errors. Counts of 10 and over are liable to be in error by one, or even two in some samples. Where there is evidence of abrasion in such shells, it is quite possible that all trace of a growth period has been removed. Such shells are therefore discarded for age studies.

It will be demonstrated that the ring described is formed probably once a year, and can be considered an age ring. It is formed by a rather long period of no growth, probably about 3-4 months. The ring has measurable breadth and is doubtless formed in the way described by Coker *et al.* (1921) and mentioned above. In the younger portion of the shell it is often possible to find sharp breaks. These may be marked by a jagged edge, showing that the former edge has been damaged, but where there has been no development of the white band of material described earlier as a ring. These marks have presumably been formed by some short-lived disturbance to the scallop, and can be ignored for age determination.

Supernumerary rings, equivalent to those which confuse the reading of fish scales, are, however, present in some scallop shells. They have every appearance of normal rings, save that they may sometimes be less well marked (Plate 1, Fig. 2). They have been presumably formed in the same manner as the "true" rings, but at other times of the year. They are more frequent in early than in late life. They are the most serious source of doubt in age determinations. Supernumerary rings may be identified as such by the irregularity of the presumed growth increments, and by comparison with the ring patterns of other shells of the sample.

In the great majority of scallop shells from the Channel, the widths of the increments (measuring from the umbo to the mid-ventral edge of the shell) are strikingly regular. The mean values of a sample fall on a very regular curve (Figs. 6 and 7); and, while there is wide divergence within most samples in the speed of growth of individuals, the shape of the curve is usually the same. Consequently, when a sample of scallop shells shows irregular increments, the reader suspects that there are supernumerary rings present. Where there is only one in the shell this may often be picked out, as the eye detects the irregularity in spacing of the rings (e.g. bottom right shell in Plate 1, Fig. 1). Where there are more suspected supernumerary rings than one, it is best to discard the shell. In practice, because of the uniformity within samples, this usually meant rejecting an entire sample.

The six specimens of Plate 1, Figure 2, are from a sample of 23 shells, of which 15 others showed five rings, one other showed four, and one other showed 10. The bottom right specimen shows four clear rings and a fifth right at the edge (hard to see because of abrasion, cf. other specimens in the same figure). The other specimens show the same five rings and one or more others as well; but in each case the extra rings are relatively faint and, if they are counted, the succession of growth increments becomes irregular. The extra rings are thus regarded as supernumerary, and the shells are taken to be all of the same age, namely 5 years, as in most of the remaining shells of the sample.

The possibility of omitted rings must be considered, but little evidence has been found to support it. One would expect to detect omissions in much the same way as the supernumerary rings, by the irregularity in the spacing of the rings.

(b) *Evidence of the Annual Nature of the Rings*

(i) *Juveniles.*—The most direct and convincing evidence that rings are formed once and once only in the year is obtained by examining the shells at all months of the year, and measuring the size of the increment beyond the last ring. The method can only be applied to the younger age-groups, because growth in the older shells is so slow (see below).

It soon became apparent that juvenile scallops were very hard to obtain. Even when fine-meshed wire netting was used in the dredge, juveniles were rarely taken. It was at first thought that this must indicate that the juveniles were concentrated on nursery beds, from which they were later dispersed. It gradually became apparent, after repeated failure to find any such nursery beds, that juvenile scallops were very rare during the period of the investigation. This is more fully discussed later.

It was then decided to preserve the shells of as many juveniles as possible. The result is a collection of 0-, 1-, and 2-group shells, i.e. shells with nil, one, and two rings respectively, aged (to anticipate the conclusions drawn below) less than 1 year, between 1 and 2 years, and between 2 and 3 years respectively. This material is listed in Table 4, and a few representative shells are shown in Plate 1, Figure 1. The samples have been divided up according to the number of rings and arranged according to the month of collection, irrespective of year. This enables the reader to follow down the right-hand column, showing the growth increment beyond the last-formed ring, where the increasing values may be noted; and also the time of year when these values are at zero, i.e. when a recognizable ring has just been formed but no further growth has been put on. In the 0-group, where there is no ring, the total length of the shell has been given as the last increment.

The division into age-groups has been somewhat arbitrary for the samples of May, June, and July. It is usually easy to be sure whether a shell has just formed a ring, but the exact month of formation is somewhat variable between localities and age-groups (and perhaps between years). Thus, of the May samples from all years, some had just formed rings, some showed no signs of newly formed rings, and some were part and part. In general, it seems that the first ring (i.e. that ring whose formation converts an 0-group shell into a 1-group shell) does not appear until the new growth of August, while the second ring is beginning to be evident in May. The age-groups in Table 4 have therefore been roughly divided accordingly.

TABLE 4

GROWTH AND RING FORMATION OF THE JUVENILE SCALLOP

Means of intermediate lengths (l_1, l_2, l_3, being lengths of shell from the umbo to the first, second, and third ring respectively), total lengths, and last increments, in mm. The samples are arranged in their supposed age-groups, and according to the month of collection. Identify areas from Figure 2

Date	Area	No. in Sample	l_1	l_2	l_3	Total Length	Last Increment
0-Group							
20. i.48	4	4				7	7
20. i.48	7	1				9	9
22. iii.46	4	2				22	22
21. iv.48		12				30	30
—. iv.48		4				27	27
20. v.47	4	2				29	29
30. v.46	7	2				23	23
30. v.47	9	34				36	36
—. v.47	8	3				33	33
1. vi.47	9	10				31	31
1. vi.47	8	8				34	34
2. vi.47	5	20				34	34
9. vi.48	6 and 7	4				31	31
—. vi.48	6 and 7	6				38	38
16. vii.47	6 and 7	4				26	26
1-Group							
2. vi.47	9	7	33			34	1
13.viii.47	9	8	30			30	0
25.viii.48	4	38	33			35	2
18. ix.45	1	2	41			46	5
20. x.45	1	10	42			52	10
20. x.45	2	2	38			48	10
17. xi.47	3	23	24			36	12
6. ii.47	1	3	38			57	19
—. iv.48		2	29			52	23
2-Group							
30. v.47	9	2	27	64		64	0
—. v.47	8	2	37	62		62	0
1. vi.47	8	1	29	71		71	0
2. vi.47	8	1	28	62		62	0
9. vi.48	8	5	36	72		72	0
9. vi.48	6 and 7	2	35	68		68	0
—. vi.48	6 and 7	2	23	67		67	0
16. vii.47	6 and 7	12	?	69		69	0
25.viii.48	4	6	34	71		72	1
—. ix.46	9	1	32	70		72	2
—. iv.48	8	1	28	71		84	13
3-Group							
—. v.47	8	1	21	47	59	59	0
25.viii.48	4	1	37	76	79	79	0
—. x.46	1	4	28	60	69	74	5
—. x.46	2	3	31	72	82	84	2

There is a great preponderance of samples taken just at this time of year, when it is often doubtful to which age-group to assign a sample. This is because the ring-forming season coincides with the scalloping season. Nevertheless there are sufficient samples from other months, particularly in the 1-group, to leave no doubt that new growth begins usually in August and that a new ring is rarely formed until the following May. Further, so far as the evidence goes, it shows that all individuals form a ring then or in the succeeding two months (Plate 1, Figs. 1 and 2).

The growth of the 1-group apparently takes place throughout the year, save for the two or three winter months of May to July inclusive. It is perhaps unwise to conclude from this that all age-groups behave similarly. Certainly the older age-groups probably start their new growth later than the younger. The mean values for l_1 (length of the shell from the umbo to the first ring) are rather constant throughout, at about 30 mm., and this agrees with the growth curves of Figures 6 and 7, and, more importantly, with the mean total lengths of the 0-group samples taken during the season of ring formation. The latter is direct proof that, at least as far as the first ring is concerned, the age determination method is valid and accurate. The values of l_2 (i.e. length of the shell from umbo to second ring) appear rather high, which is no doubt due to the selective action of the dredge in taking larger scallops and losing the small ones. Such selective effect would not be so great in the 0-group, where all specimens would stand an approximately equal chance of escape through the meshes, since even the largest of this age-group are relatively small. The three samples from area 1 (Tinderbox) in the 1-group are worth noting, since they show a very consistent mean l_1, and a steady increase in mean total length over the months.

It is of interest to consider some possible cause of the ring formation (cessation of growth) and of the subsequent new growth. The following comments are tentative. In other lamellibranchs (including Pectinidae), ring formation seems to be associated with critically high or low temperatures, or with spawning.

Gross observations on scallop condition were made monthly over a period of 2 years, and it seemed probable that spawning by any one individual is spread over a period of 3-4 weeks. Generally speaking the main spawning period occurs during August, but there are wide fluctuations around this period. Scallops with groups of mature eggs or spermatic tubules scattered throughout the gonad may be encountered any time after August, but these, it has been found, are undergoing resorption. Following the release of the sex products the female moiety of the gonad loses its colour and the whole organ, together with the adductor muscle, becomes soft and "watery". In the early autumn, after this period of quiescence, the gonad begins to change with striking rapidity; it reassumes its distinctive colours, becoming firmer, and the adductor muscle also becomes firm. This must cause a considerable drain on the resources of the animal.

It is probably this reorganization of materials in the body of the mollusc that results in a stoppage of shell growth and formation of the ring. During the ensuing 2-3 months (including the early portion of the fishing season) condition is usually improving, and the gonad increases in size and firmness.

Water temperatures in the Channel are minimal between June and August. It appears likely that the beginning of spawning follows shortly on the first rise of water temperatures.

Shell growth begins about August and September. It is possible that, whereas the preparation for spawning caused a drain on the soma and cessation of shell growth, the act of spawning might not call for any great effort, the gonads merely expressing their previously stored materials. In the sexually immature scallops, with which Table 4 deals, there is no question of spawning acting as a drain on the soma. It may be questioned whether there is in those individuals any change in metabolic activity at all between April and August. Possibly the immature scallop is subject to a foreshadowing of the metabolic changes associated with spawning, such as was shown by Hickling (1935) to take place in the immature hake (a fish).

Finally, it may be significant to note that plankton net hauls in the Channel show a rather regular efflorescence of diatoms and dinoflagellates from about September to November—somewhat after the onset of shell growth in the young scallops, but perhaps providing a useful abundance of food at a critical time.

(ii) *Adults*: *Growth Curves*.—To test the validity of the rings as age rings in the older shells, it is necessary to assume the hypothesis and determine whether the results obtained justify it.

The widths of the growth zones have been measured in a number of samples. The width of a zone is taken as the distance from the umbo to the most ventral limit of the ring enclosing it. These widths will be referred to as l_1, l_2, l_3, etc., as in age work on fish.

Figures 6 and 7 illustrate some typical growth curves obtained in this manner. The curves have been drawn by eye and smoothed, so that the lines do not necessarily pass through each point. It will be seen, however, that the points representing mean shell sizes at successive ages do in fact fall on or very close to the smooth curves. Figure 7 illustrates the manner in which the older age-groups have an apparent slower growth rate than the younger, at the same locality. In Figure 6 this effect has been avoided by taking the averages of the mean intermediate lengths of several age-groups in each sample; by this means the growth rates of different localities may be compared without so much concern as to the effect of the particular age-groups employed.

To a worker accustomed to handling the growth curves of sea fish, these curves show some striking features. Firstly, there is the very great change in growth rate between the young and the old specimens, sometimes but not always involving a sharp point of inflexion in the curve. There is a remarkable difference in rate of growth between the localities. The younger age-groups appear to grow faster (see below). And lastly, the individuals of one age-group from one locality invariably show a considerable range of size, yet in spite of this the mean growth curves of samples from one locality are extremely regular, and this is strikingly true also of the growth of the individuals.

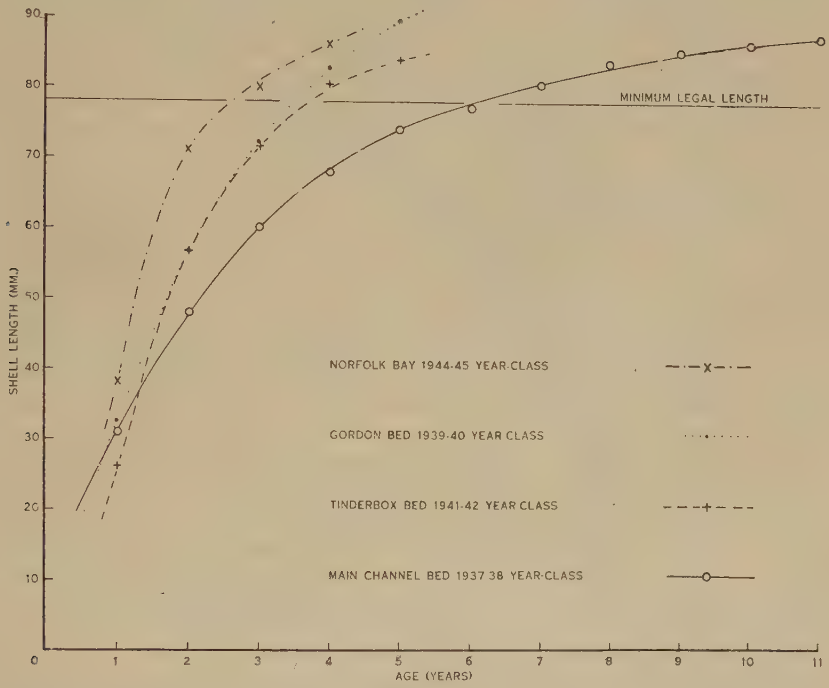

Fig. 6.—Growth curves for commercial scallops of the stated localities and year-classes, calculated from shell lengths attained at the time of formation of the successive annual rings (i.e. from "intermediate lengths"). The plotted intermediate lengths are the means of the mean values for the different age-groups in the year-class. For further information see text.

These features are all characteristic of the growth of lamellibranch shells. Comparison may be made with the works of Weymouth (1923) on the Pismo clam, Orton (1926) on the cockle, Chamberlain (1930) on various species of freshwater mussels, Weymouth, McMillin, and Rich (1931) on razor clams from widely separated localities, Weymouth and Thompson (1931) on the Pacific cockle, and Coe and Fox (1944) on the California sea mussel. The last paper is of particular interest, in that the authors kept marked mussels in cages, and found that even within the one cage growth was extraordinarily uneven, first one and then another individual putting on a spurt of growth.

The results of Stevenson (1934) and Tang (1941) for two species of the Pectinidae are also in accord with the results presented in this paper.

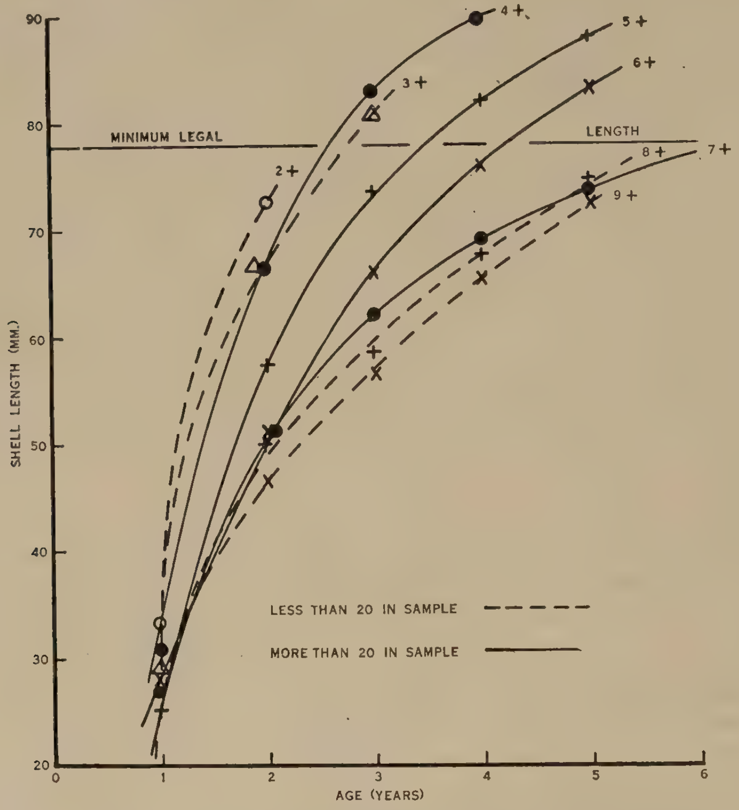

Fig. 7.—Growth curves for commercial scallops of the separate age-groups in a sample collected at Barnes Bay in September 1946, showing the apparent variation in growth rate between age-groups. The symbols 2+, 3+, etc. refer to the 2-group, 3-group, etc., i.e. to scallops of slightly more than 2, 3, etc. years of age. Broken lines indicate that there were less than 20 specimens in the age-groups. For further explanation see text.

Locality differences in the growth rate of the Tasmanian scallop are presumably environmental. The scallop seems to do well on muddy bottom (parts of area 4, Barnes Bay) or on the more usual bottom of sand and broken shell. It would seem that fluctuations in tidal currents affect the growth of the scallop. But since the beds of the best scallops are the most heavily fished, it is impossible to determine certainly the best areas for scallops in the Channel. However, areas 1, 8, and 10 seem to produce samples showing the quickest growth, while in areas 4 and 6 the average growth is poor (see Fig. 2). This distribution suggests that the flow of water through the narrow necks of Tinderbox (north end of the Channel), Middleton-Gordon, and between Woody Island and the shore, is beneficial.

TABLE 5

SCALLOP INTERMEDIATE LENGTHS (MM.)

Means of l_1, l_2, l_3, and l_4, in material of the stated age-groups (age-group 2 indicates material of between 2 and 3 years of age, age-group 3 between 3 and 4 years, etc.) in samples collected in 1946

Area (see Fig. 2)	Date	Age-Group	l_1	l_2	l_3	l_4	No. in Sample
9 Gordon	Sept. 1946	5	24.8	63.7	79.4	87.6	25
		6	27.0	63.8	80.4	88.8	29
		7	33.0	57.2	72.2	83.0	26
		8	32.3	55.3	71.0	83.1	25
		9	31.8	55.4	68.1	79.8	9
9 Gordon	Oct. 1946	5	23.9	58.1	72.1	81.2	24
		6	24.2	57.9	73.8	80.6	26
		7	29.8	50.7	67.6	79.1	29
		8	31.0	51.4	67.2	77.6	25
8 Main Channel	Dec. 1946	7	32.6	51.1	63.5	72.4	34
		8	31.5	50.6	63.4	73.1	25
		9	30.6	49.4	62.5	71.8	19
6 Simpson's Point	Sept. 1946	6	31.4	49.0	60.2	67.8	13
		7	33.0	51.3	61.9	69.9	22
		8	33.4	52.2	63.5	70.4	47
		9	31.0	47.9	59.6	67.7	45
5 Apollo Bay	Sept. 1946	7	29.8	49.4	61.6	69.3	40
		8	31.0	48.5	59.3	68.2	59
		9	29.9	47.7	59.1	67.0	46
4 Barnes Bay	Sept. 1946	2	35.2	72.7			14
		3	29.2	66.3	81.1		13
		4	30.2	66.5	82.9	89.6	31
		5	25.9	57.1	73.3	84.0	21
		6	26.7	50.8	65.8	75.6	20
		7	27.8	50.3	61.7	69.0	24
		8	30.5	50.9	58.3	67.6	15
		9	29.8	46.9	56.4	65.1	12
1 Tinderbox	Sept. 1946	4	25.7	53.9	66.9	71.8	48
		5	25.2	53.1	64.3	70.3	26
		6	26.2	49.7	61.5	68.9	25

There is no need to give all the detailed analyses of growth rates. Table 5 has been drawn up to supplement the figures. Here, as in Figure 7 (which is based on some of the data of Table 5), the familiar phenomenon of apparent faster growth by the younger age-groups is clear. This is no doubt due to the fishery removing the fast-grown individuals of each age-group first. This would occur, firstly through a tendency for the small specimens to escape through the meshes of the bag of the dredge, and secondly by the scallopers deliberately culling out and returning to the water the smaller specimens (below legal size). The 1946 Barnes Bay sample (Fig. 7) is a striking case. Probably other localities would show

TABLE 6

FREQUENCY DISTRIBUTIONS OF INTERMEDIATE SHELL LENGTHS (l_1, l_2, l_3, AND l_4) FROM FOUR SAMPLES OF ADULT SCALLOPS, AND OF TOTAL SHELL LENGTHS FROM TWO SAMPLES OF JUVENILES (CF. TABLE 4): SAMPLES SELECTED FOR LARGE SAMPLE SIZE

Length (mm.)	Area 1 (Tinderbox) 1946, 4-Group				Area 2 (Sheppards) 1946, 4-Group				Area 4 (Barnes Bay) 25.viii.48, 1-Group Total Length	Area 9 (Gordon) 30.v.47, 0-Group Total Length	Area 8 (Main Channel) 1946, 7-Group				Area 8 (Main Channel) 1946, 8-Group			
	l_1	l_2	l_3	l_4	l_1	l_2	l_3	l_4			l_1	l_2	l_3	l_4	l_1	l_2	l_3	l_4
18	3																	
21	7								2						1			
24	15								1	1	2				2			
27	12				1				3		1				2			
30	7				3				2	3	6				3			
33	3				8				9	9	14				13			
36	1				8				6	9	11				4			
39					8				6	10								
42		1							4	1		2				1		
45		2							5	1		2				3		
48		9										8				6		
51		12										10				6		
54		8				1						7	1			7		
57		3	2									4	5			2	2	
60		7	4			1						1	5				8	
63		3	13	4		5							9				6	
66			12	5		7							6	6			4	2
69		2	7	16		5	3						5	9			4	5
72			4	8		5		1					2	4			1	7
75		1	2	7		4	4	1					1	8				7
78			1	3			8	5						5				2
81			1	1			6	5						1				1
84				2			3	7										1
87			2				4	5						1				
90				1			1	3										
93				1														
96																		
99								1										
Mean	25.7	53.9	66.9	71.8	35.1	67.9	79.4	83.3			32.6	51.1	63.5	72.4	31.5	50.6	63.4	73.1

equally striking examples if they involved the same range of age-groups. Table 5 shows that the phenomenon was well marked in the 1946 Gordon samples. Some fishing had been taking place there in that year. In the main Channel, however, fishing had been less intense and it is not so well marked. At Apollo Bay and Simpson's Point there had been no fishing, and the phenomenon is slightly noticeable or absent. At Tinderbox there had been intensive fishing, but this sample does not show the phenomenon to a marked degree. The variation in growth rate of scallops gives great scope for this effect to become apparent.

A close study of the later growth increments is not very rewarding. There are indications that growth is better in some years than others, but the record is confused by the liability of part of the shell to be eroded, and by the uncertainty of age determination among these older specimens.

Table 6 is a selection from the material to show the manner of the distributions of the intermediate lengths. Evidently the distributions do not usually approximate to normal curves. The same is true of the total lengths of individual age-groups from one locality although some composite curves for all the specimens (i.e. mixed age-groups) from a single locality may approximate to the normal curve, as in Figure 8. Table 6 should be compared with Table 4 to show the general correspondence in the size of l_1-l_3, though the values in Table 4 are probably affected by selection of the larger individuals of the age-groups. The two largest samples of Table 4 are included in Table 6 to show that the complexity of the length frequency curves is apparent at an early age, and presumably reflects the prolonged spawning season.

The above-mentioned tendency for some of the total length frequency material to form normal curves, as in Figure 8, is probably brought about, in part, by growth compensation—slow-grown specimens tending to go on growing longer.

(iii) *Adults: Length Frequency Polygons.*—In the early phase of the Tasmanian scallop investigation large numbers of length frequency data were obtained monthly on six representative scallop beds, for a period of from 2 to 3 years. The data are copious and need not be reproduced here.

It was found that the general size distribution of the scallops is fairly constant on each bed (Fig. 8). For instance, the scallops from Apollo Bay (area 5) were always small, the length frequency polygons were compact, and the mode varied between 75 and 81 mm.; the Barnes Bay (area 4) scallops showed a great size range in each sample, usually with more than one mode, varying between 54 and 91 mm.; the Gordon (area 9) scallops were usually large, but there was much variation between samples, apparently as a result of sampling different, closely spaced populations on the various visits—the modes varying mostly between 78 and 99 mm.

In all this material it is impossible to find any series of polygons divisible into consistently spaced modes, nor is there any series showing a steady progression of the mode(s), such as one would expect with a population of growing individuals.

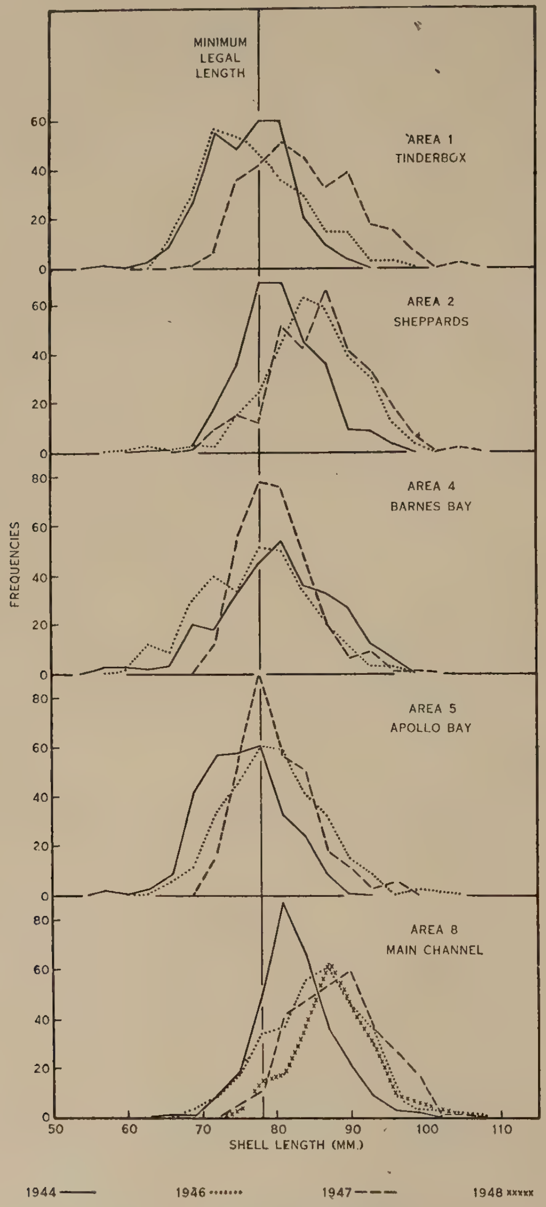

Fig. 8.—Length frequency distributions of commercial scallops measured in different years at each of five localities. For further explanation see text.

These facts are consistent with the explanations previously suggested, namely that size is virtually no criterion of age, so that, in the absence of very young age-groups, separate age-groups do not become apparent in the length frequency polygons; and since the scallops in the older age-groups grow only a few millimetres in the year, one would not expect any progression of the modes to become apparent.

TABLE 7

NUMBERS AND MEAN LENGTH INCREMENTS OF SCALLOPS TAGGED IN 1946 AND RECOVERED IN 1947

Area	No. of Recoveries	Mean Increase in Length (mm.)
1	5	3.2
2	14	3.7
4	3	6.0
8	110	1.2
9	9	4.4

(iv) *Adults: Experimental Evidence.*—In an attempt to measure directly the growth of the scallop shell, several specimens were measured, marked, and confined in a cage of wire netting for about 12 months. The cage was sunk to the bottom in about 5 fathoms of water on a recognized scallop bed. It was recovered on several occasions, and the scallops measured. It soon became apparent that not only were the scallops not growing appreciably, but that the shell length of a number had actually decreased by 1-2 mm. This was at first thought to be due to inaccurate measuring; but by the end of 6 months the true explanation became evident—that the scallops, in continually swimming around inside the cage (ventral edge foremost) were rubbing off the brittle edge of their shells on the rough galvanized wire. The edges were thick and clean and had a "raw" look. The conclusion was, therefore, that any growth was insufficient to gain on the leeway caused by the abrasion of the shell on the wire.

The data from tagging are more satisfactory. In the course of tagging experiments in the Channel (see Tubb 1946) a number of recoveries have been received of scallops which were at liberty for a period representing two winter (slow growth) seasons and one summer season. These are the specimens tagged in 1946 and recovered in the fishing season of 1947. Table 7 summarizes their mean increase in length. It is to be noted that some showed a reduction in size (cf. Tubb 1946); these have been included in the means.

The ages of the specimens are not known. But it is probable that the samples from areas 8 and 9 contained no specimens aged under 5 years, and that the high growth shown for area 4 is due either to one of the three specimens being a young scallop, or to the data relevant to it having become confused with those of another specimen.

Reference to Figures 6 and 7 shows that the growth indicated by these tag returns is of the same order as that derived from the study of the later growth rings. This evidence is direct and strongly confirmatory.

(*c*) *Summary of Evidence of the Annual Nature of the Rings*

The annual nature of the earliest rings is demonstrated by comparing very young shells at successive seasons of the year, and noting that all shells lay down a ring once only in the year. This technique cannot be used on the older shells because their growth is very slow. In these shells there is the direct evidence of recoveries of tagged shells to show the order of growth.

When the growth rings are taken as age rings and the results so obtained are analysed, their very reasonableness and regularity offer strong support for the validity of the assumption. Many phenomena can be explained from the results so obtained, and the general characteristics of the growth of the scallop are found to agree with those of other lamellibranchs. Moreover l_1 and l_2 are found to agree very well with the total length of young specimens presumably in their first and second winters.

This method of age determination is sufficiently accurate for the use to which it will later be put. Absolute accuracy is not claimed for ages over about 10 years, and some samples are considered too vague and confused by "interruption" rings to warrant any estimation of age.

VII. THE AGE AND SIZE COMPOSITION OF THE "COMMERCIAL" SCALLOP STOCKS

(*a*) *The Age Composition of the Stocks*

With a technique for determining age, the stocks of scallops can be analysed with results as given in Table 8. The samples from each bed have been divided up according to age, and the numbers in each age-group listed.

The 1946 samples were all taken after the 1946 scalloping season. In preceding years fishing had been heavy in areas 1, 2, and 4. In 1946 area 4 was again fished heavily for a short while until it became unproductive. Areas 1 and 2 appeared to be no longer profitable. It was in 1946 that area 8 began to be heavily worked, the boats covering the whole breadth of the Channel in this part though concentrating, as always, more in some parts than others. In 1947 and 1948 fishing continued heavily on area 8, almost to the exclusion of other beds, though in 1948 a minority of the boats also worked areas 9, 10, and 12. Area 10 received particularly heavy fishing for its size. The northern beds were untouched except when the weather prevented dredging elsewhere. In 1949 area 8 in turn appeared to have become less profitable, and the fishing effort was spread over areas 6, 7, and 9. The 1949 samples are therefore mostly drawn from these beds. The 1949 samples were selected during the season from the scallopers' catches.

Included in Table 8 is the age analysis of a small sample of scallops taken in Norfolk Bay (Frederick Henry Bay) outside the Channel (Fig. 1). This was a new bed fished towards the close of the season in 1948 and not at all in 1949. It is interesting to note that here the dominant 4-group is of the same year-class as the local concentration of 5-group scallops taken in area 7 in the next year.

Two of the 1946 samples contained many shells which were almost wholly illegible, owing to numerous interruption rings. However, they also contained several young scallops with clearly marked ages. The figures for these younger ones have therefore been included; but the majority were clearly old scallops, and the figures in Table 8 are, therefore, not in any way representative of the age-groups in these two samples.

Bearing in mind the course of the fishery in the years outlined above, it is clear that in 1946 the important samples are those from area 8. These were principally of 7- and 8-year-old scallops. The samples from the two unfished beds, Simpson's Point and Apollo Bay (areas 6 and 5 respectively), were about the same, with maximum ages of about 10 years. The absence of young scallops will be noted. This suggests that there had been a successful spawning 7-9 years previously (1939-41), but not since. There were, however, some younger scallops on the northern beds. Here there had been heavy fishing in previous years. It may be mentioned that young scallops have been a marked feature of catches from off Woodcutters Point (area 4) throughout the course of these investigations.

The sample from 1948 shows that the dominant age-groups of area 8 were 10 and 11, and the maximum ages were 13 and 14 years. This is a somewhat greater advance in age on the 1946 series than one would expect, but the data are from a single large sample which may not be representative.

The 1949 samples from corresponding areas show dominant age-groups at from 9 to 11 years. This is in better agreement with the age composition of the 1946 samples, assuming that the stock has simply become 3 years older, and that there has been selective catching of the larger and older members. The samples from area 6 are also in good agreement with those from 1946, indicating that the stock has remained stable and has simply aged by 3 years. In all the 1949 samples, the only ones showing a substantial influx of young scallops are those from Middleton (area 7).

The conclusion is that over this period there has been virtually no recruitment of juveniles to the adult stock of scallops. The fishery has been relying on a series of good spawnings which occurred from about 1939 to 1941.

TABLE 8

AGE COMPOSITION OF THE "COMMERCIAL" SCALLOP POPULATION IN 1946 AND 1949, WITH TWO SAMPLES FROM 1948

In two of the samples (see bracketed figures) the age analysis is incomplete; for further explanation see text

Date		Area	Age in Years																
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Uncertain
—. ix.46	9	Gordon		1		3	26	29	46	57	9	1							9
—. x.46	9	Gordon					21	25	28	78	8	2	3						
—. xii.46	8	Main Channel					2	8	34	29	18	2		1					
—. ix.46	6	Simpson's Point						13	22	47	45	12	1						36
—. ix.46	5	Apollo Bay					2	12	40	60	46	6							13
—. ix.46	4	Barnes Bay					(26)	(34)	Incomplete										140
—. ix.46	2	Sheppards			(3)	(28)		Incomplete											169
—. ix.46	1	Tinderbox			4	48	82	24	4										
—. iv.48	8	Main Channel			1			2	6	16	21	52	50	26	11	9	1		
6.viii.48		Norfolk Bay				19	6												
5.viii.49	10	Woody Island									15	2	3						
5.viii.49	9	Mountain Creek							2	16	45	15	3						12
5.viii.49	9	Sheepwash					1			13	21	10	17	1					7
5.viii.49	6	Great Bay									3	4	8	13	32	10	3	2	7
5.viii.49	6	Simpson's Bay											1	10	9	10	8		4
5.viii.49	7	Middleton	1			1	21			17	6	8	5	4	1				
5.viii.49	6	Adams Bay									1		9	8	7	9	3		1

(b) *The Size Composition of the Stocks*

Figure 8 shows length frequency distributions of scallops taken at five localities on the following dates: November-December 1944; April 1946; April 1947; and, for one locality only, April 1948. The polygons have been drawn from the unsmoothed frequencies of successive 3-mm. size-groups in the samples, which were all about the same size (200 individuals).

The polygons are quite typical for the commercial scallop; some are unimodal, some multimodal, and some approximate to the normal curve.

One feature is common to all localities (except possibly Barnes Bay); the later the year of sampling the larger the scallops at each locality . In most, this shift towards the right of the graph is best shown at the left-hand side of the polygon. It cannot be seen so clearly by comparing the modes and the right-hand sides of the polygons, doubtless because of the selective removal of the largest scallops by the fishery. Incidentally, the order of growth indicated by the shift of the polygons agrees with the calculated rate of growth of the older scallops, as determined from the rings.

The important point here is that there is no indication, except in the Barnes Bay samples, of any recruitment of juvenile scallops. The populations are stable: the animals grow slowly in size, and there is some selective fishing of the larger specimens. Otherwise there is no change.

VIII. DISCUSSION

The sampling for age composition since 1946 shows there has been no worth-while influx of young scallops into the areas being fished. The sampling for length composition goes back further, to 1944, and is quite independent of any subjectivity there may be in the age determinations; this, too, shows that there has been no substantial recruitment.

Further, as a matter of observation, there has been a dearth of very young scallops ("buttons") over the period of this study (1946-48). At first this was thought to mean that the young were concentrated in nursery beds, but intensive search failed to reveal any such beds. Two particular instances are worthy of note. In 1947 the writer was directed to a supposed nursery bed off Mountain Creek (area 9). Dredging here brought up large numbers of dead 1-group shells, but no live ones. Again, he was advised of young scallops between Flowerpot Rock and Whaleboat Rock (area 7); no success was had here either, but it may be significant that in 1949 some samples of 5-group scallops were obtained from this locality (see Table 8).

It is evident from discussions with scallopers that they are interested in young scallops, and note them when they are available. Experienced scallopers agree that there has been a dearth of "buttons" for some years. Apparently the young may collect in patches to some extent, but there are many reports of their being widely scattered when they are present in any quantity.

The failure to find young scallops by special searching, and the absence of young scallops in the catch, indicate that recruitment has been very low for some years past in the whole Channel. The question remains whether this adverse fluctuation is man-made, and can be corrected.

Contamination of the waters of the Channel can be dismissed as a possibility. Presumably the scallops have been actively spawning over the period of dearth, and the question is one of survival of the larvae or metamorphosed young.

It has been suggested that the constant stirring or ploughing of the bottom by the dredges is to blame. This could be due to the nature of the bottom being made no longer suitable for the metamorphosing larva, or to actual mechanical disturbance killing the metamorphosed 0-group. The life history and requirements of the larva are unknown. But against this view is the fact that large scallop-bearing areas of the Channel were entirely free of dredging between 1942 (when, as indicated in Section VII (*a*) above, the poor survival years apparently started) and 1946. Presumably these undredged areas remained as suitable as ever for settlement and subsequent survival of the young scallops.

It could be argued that the Channel was dependent for its supply of young (0-group) scallops entirely on the northern beds, or on beds which were being fished from 1942 to 1946—the young scallops reaching the other beds by swimming—and that, when these beds were rendered unfit for the young by the constant dredging or when the adult concentration on these beds had been excessively reduced by fishing, the supply ceased altogether. Apart from its inherent unlikeliness, this possibility is directly ruled out by the above-mentioned reports of the young scallops being spread apparently all over the Channel (though no doubt collecting more in some places than in others) in previous years. Therefore the present adverse fluctuation is probably a natural one, although the cause is unknown.

Early in the paper it was adduced from the verbal and written history of the fishery that there have been several major natural fluctuations in the size of both the doughboy and commercial scallop populations in the Channel within the last 30 years.

Cataclysmic natural population fluctuations are common in lamellibranchs. Attention may be drawn to the virtual disappearance of the mud oyster (*Ostrea sinuata* Lamarck) in Tasmania. It is known from the study of middens that the Tasmanian aboriginals consumed vast numbers of these oysters and even within recent history mud oysters have been far more common than they are now (see Section IV). The literature contains many other examples of which Dexter (1944) gives an admirable summary. Most of these accounts are couched in general terms, the shellfish being described as occurring in dense beds, or sparsely, or not at all. It is clear that catch statistics are not required to indicate fluctuations of this degree. Field (1922) states that mussel beds of the Atlantic coast of North America last for from 3-4 years, after which mussel fishermen must look elsewhere; beds may reestablish themselves after an interval. Hagmeier (1930) describes the sudden appearance of a population of *Mactra subtruncata* da Costa, presumably as the result of a favourable spawning, following which the larvae were distributed over a favourable area of bottom just at the time when they were seeking bottom; this population was later invaded by predators and considerably reduced in size. Coe (1946) was able to follow through the sudden appearance of a population of the California bay mussel.

The population of commercial scallops on which the Tasmanian scallopers have been dependent over the past decade apparently began to develop about 1937. There was then, and for several subsequent years, a particularly heavy population also of the doughboy but by 1944 this species had become relatively sparse. The year 1941 or 1942 saw the last abundant brood year of the commercial scallop, and the fishery has been dependent on the progeny of this period (*c.* 1937-42) ever since. The doughboy is probably a short-lived species, and it may be that both species began to fail about the same time. For several years past the scallopers have simply worked a commercial scallop bed, or a number of beds, until they became unproductive; they have then moved on to new beds. When no more beds remain untouched, it will probably be necessary for scallopers to charge a considerably higher price for their catches if they are to obtain a livelihood from the remnants of the old beds.

When the scallop investigation began, overfishing had been mentioned as a probability. This was deduced from the gross catch and effort statistics. The regular and apparently intelligible changes shown by these figures (Fig. 5) have been shown above to be to some extent (but not wholly) deceptive, since two species are involved and are not distinguished in the records. Nevertheless the prospect of managing the stocks and protecting them from overfishing was at first uppermost in the writer's mind. To manage a stock means, *inter alia*, to try to balance the fishing mortality and natural mortality against growth and recruitment. But if recruitment is negligible the overfishing of bed after bed is inevitable, and to talk of management is meaningless.

The commercial scallop population in the D'Entrecasteaux Channel is suffering primarily from an adverse natural fluctuation in abundance—a severe long-term shortage of recruits—and secondarily from the overfishing of bed after bed (i.e. of the isolated subpopulations of adults), as the fishermen vainly try to maintain their rate of exploitation of the dwindling resource. Unless this condition is soon checked by the reappearance of ample numbers of recruits, the fishery may come to an end.

In face of this, there are three considerations to bear in mind. Firstly, that, so long as a fishery exists, research can perform a useful service to the trade by watching the survival and influx of young scallops, and giving notice of impending improvement (a good recruit year may occur at any time) or further deterioration in the condition of the stock. Secondly, that, from a study of the requirements of the larva, it may be found possible to cultivate the scallops by rearing them beyond a critical age, much as oysters are farmed in Australia and elsewhere or clams in North America (Moore 1948). Thirdly, if the fishery is allowed to continue without interference, is there a possibility that there will be an insufficient seeding of scallops from which the area can become restocked, even if favourable conditions return?

The last is the crucial problem. Gross and Smyth (1946) draw attention to the fact that, in spite of the enormous fecundity of oysters, former natural oyster beds in the vicinity of artificial oyster beds have not become restocked from the spat of the artificial beds. Korringa (1946) suggests that *millions* of oysters, not thousands, would have to be used to start a natural oyster bed, in order to ensure fertilization of spat, produce enough spat (since only about 1 per cent. in a good locality such as the Oosterschelde will successfully settle), and provide cultch (the clean growing edge of oyster shells).

The question of providing cultch does not apply to the scallop, but it is certainly possible that there might at some future time (or even now) be a large population of scallops left in the Channel and yet be too widely scattered to ensure fertilization of the ova.

It is as yet only possible to guess at the answer to this question. But there are some factors which favour the continued supply of scallop larvae: (1) the D'Entrecasteaux Channel is a more or less stable body of water, particularly over the main period of spawning of the scallop, so that a good proportion of larvae is likely in most years to be retained within the Channel and not uselessly dissipated; (2) provided the law governing the minimum size at which scallops may be caught is rigidly enforced, the proportion of scallops which never reach marketable size (see Figs. 6-8) would serve as a fund of spawning individuals; (3) under present marketing and price conditions, it is apparently uneconomic for the scallopers to work on a bed unless there is a rather high concentration of scallops there.

A danger is that, with the scallop stocks in a depleted condition as the result of heavy fishing combined with little or no recruitment, a disease might break out and further reduce the population.

The best policy seems to be, then, to warn the trade of the uncertain future and meanwhile to watch the catch, the incidence of fishing, and conditions in the trade generally, to detect any changes which might further reduce the population to a dangerously low level.

(Since Mr. Fairbridge wrote this paper some beds of juvenile scallops have been located. The sizes of the beds suggest that they will not sustain the fishery for more than a part of a season. However, their presence indicates that the Channel population has not lost its capacity for reproduction, and that there could still be a return to years of good broods.)

IX. Acknowledgments

It is desired to thank the officers of the Fisheries Division of the Tasmanian Department of Agriculture for their practical help and encouragement in the scallop investigation; a special tribute to the late T. J. Challenger, former Inspector of Fisheries, is especially warranted.

The photographs in Figures 3 and 4 were taken by Mr. A. M. Olsen of the Division of Fisheries, C.S.I.R.O.; Plate 1 and the line figures are the work of Mr. R. Breach of the same Division.

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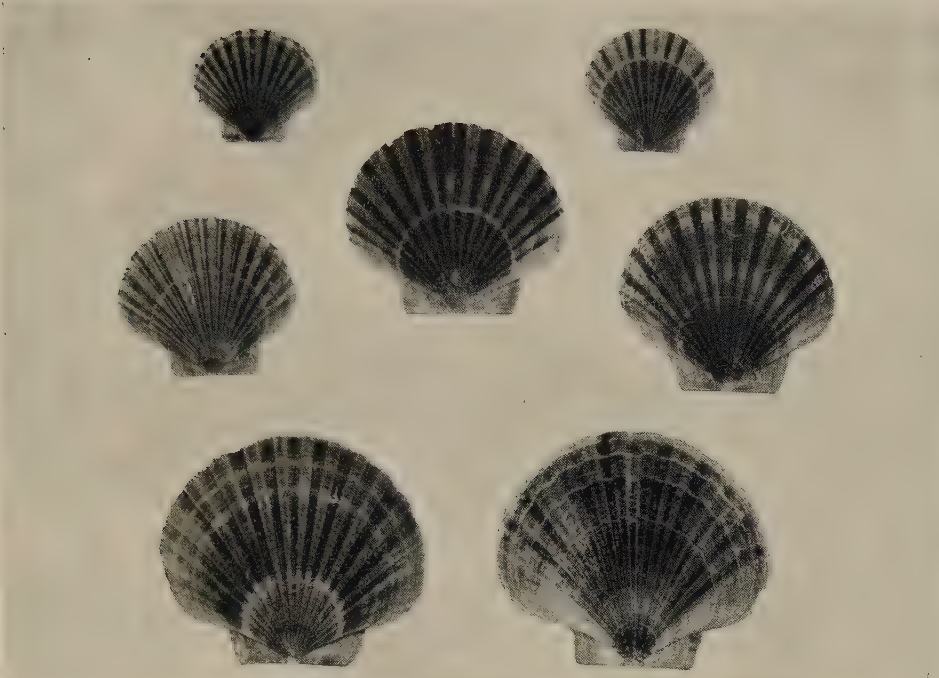
EXPLANATION OF PLATE 1

Fig. 1. A selection of scallop valves. Top left: 1-group shell of late August, with first ring not long formed. Top right: 1-group shell of mid November, with further growth outside the ring. Middle left: 1-group shell of early February, with still further growth outside ring. Middle centre: shell of early June aged about 2 years, with very wide growth outside the first ring and formation of second ring imminent (Mr. Fairbridge regarded this shell as having a second ring forming at the margin, although that is not evident in the photograph). Middle right: 2-group shell of late August, with second ring not long formed. Bottom left: 3-group shell of October, with new growth outside the third ring. Bottom right: 4-group shell (the small first ring is supernumerary) of mid August, with fourth ring not long formed.

Fig. 2.—Six scallop valves from the same (July) sample; these are all considered to be 5 years old (the fifth ring just at the edge) although in all but the bottom right specimen the record of age is confused by fainter, irregularly spaced supernumerary rings. Note abraded edges. See text for further remarks.

THE TASMANIAN "COMMERCIAL" SCALLOP



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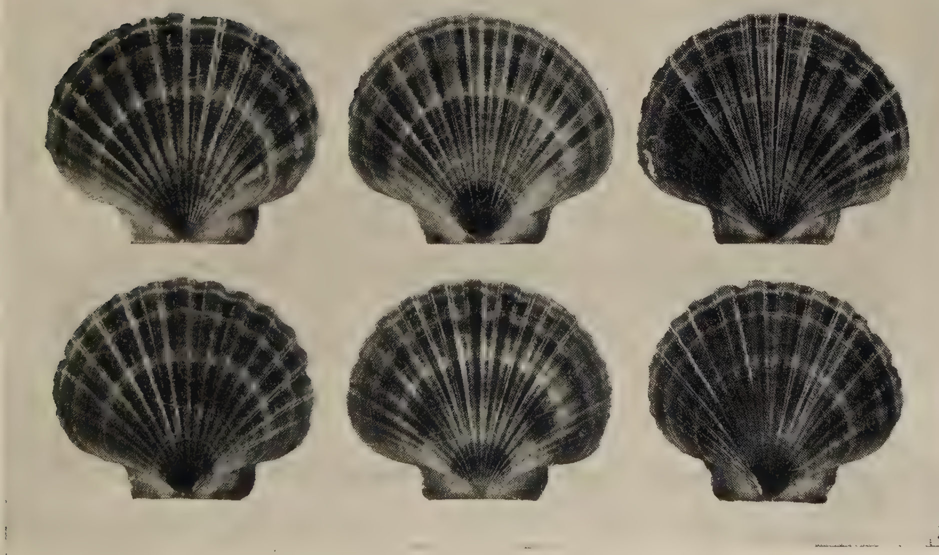

2

STATUS OF THE FISHERY FOR SEA MULLET (*MUGIL CEPHALUS* LINNAEUS) IN EASTERN AUSTRALIA

By J. M. THOMSON*

(*Manuscript received August* 14, 1952)

Summary

Various shortcomings of the statistical systems in vogue in the fisheries of the eastern States of Australia are discussed from the viewpoint of a biologist. It is impossible to compute an estimate of the catch per unit of effort involving a time factor. The annual mullet catch for the whole eastern seaboard has remained substantially about 11,000,000 lb. for the past 10 years, but the total caught in any subdivision of the area has fluctuated widely. The Clarence River, Port Macquarie, Maryborough, and Wallis Lake areas are the most important producers. There is a high degree of correlation between the fluctuations in the mullet catch and those in the total catch of estuarine fish. The size and age composition of the mullet catch have shown only slight variation over the last 10 years, and there is no significant variation in this respect from the composition in 1903. The fluctuations in catch and catch per man are not inconsistent with theories of overfishing nor with those of natural population cycles; but the only theory which receives confirmation independently of the curves of catch and of catch per man is an economic one. Competition from both the trawling industry and the import industry has been responsible for the characteristics of the estuarine catch curves. It is estimated that the weight of fish flesh to be gained from recent changes in the management of the fishery could at best be considerably less than the amount of annual variation in the catch.

I. INTRODUCTION

A preliminary statement of the biology of *Mugil cephalus* Linnaeus, the sea mullet of eastern Australia, by Kesteven (1942) included a section on the condition of the fishery and concluded with suggestions for its control. No definite diagnosis of the condition of the fishery was possible owing to the lack of catch figures, other than the total catch of all species, in New South Wales, which is the most important producer of mullet.

Since that time a statistical system has been inaugurated, and, although the precise history of the fishery has been forever lost, the trends over the last 10 years can be reported upon and some inferences drawn on the previous course of the fishery.

II. ANNUAL CATCH

(*a*) *Critique of the Statistical Systems*

As much of the data on the fishery depends upon the statistics of catch, it is necessary to explain the origin and choice of certain of the data used in this paper.

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In New South Wales the early reports gave catch figures which were only handlings in the Sydney markets. The catch marketed in Newcastle was not recorded until 1900, and not listed regularly until 1910. The volume of local sales, i.e. fish not consigned to the central markets in Sydney, Newcastle, or Brisbane but sold in the neighbourhood of the district concerned, was not recorded until 1911. The amount of fish sent from the Tweed River in northern New South Wales was not listed until 1915, although, with other reports of local production, it had been reported intermittently in inspectorial reports since 1892. It was not until 1921 that a return of fish actually produced from each river or district, as distinct from the amount reaching market, was published. The accuracy of these figures is uncertain, as they were compiled from the local inspector's knowledge coupled with the railway returns of the amount of fish shipped away. It is certain that from the start the fish catch of New South Wales has been understated. Until 1939 the recorded catch was the total of all species, but in that year the separate listing of the more important species commenced.

The units in which the catch is recorded have varied through the years. Until 1921 the unit was the basket, which the Annual Reports of the Department state contained approximately 84 lb. of fish. In 1922, with the passing of the Sydney Corporation (Fish Markets) Act, the marketing system was reorganized and boxes of 70 lb. average capacity were used. Errors have been made in discussing the course of the New South Wales fishery by persons equating the capacities of boxes and baskets in using data extracted from the published tables. It seems quite clear from the contemporary evidence that it is an error to do so. Differences between the figures listed here and those published in other papers (e.g. Kesteven 1942, 1946) are due to this cause. Under the Act of 1922, all fish had to be sold by weight instead of by the basket or box, as previously. This requirement gave much more accuracy in estimating the catch, although the district returns continued to be recorded in terms of boxes until 1942. Since 1937 the district catches have been compiled from fishermen's returns checked against transport returns, but there is obviously the opportunity to make local sales which are not reported, and it is probably a fact that the published figures are still somewhat under the true values. Nevertheless, considering the active policing by the departmental inspectors to ensure that fish are marketed through a recognized market, the amount concerned cannot be large.

During the years of the recent war there was added incentive to make a true declaration of the amount of fish taken; as both continued release from military duties and the allotment of a petrol quota depended upon good fishing results.

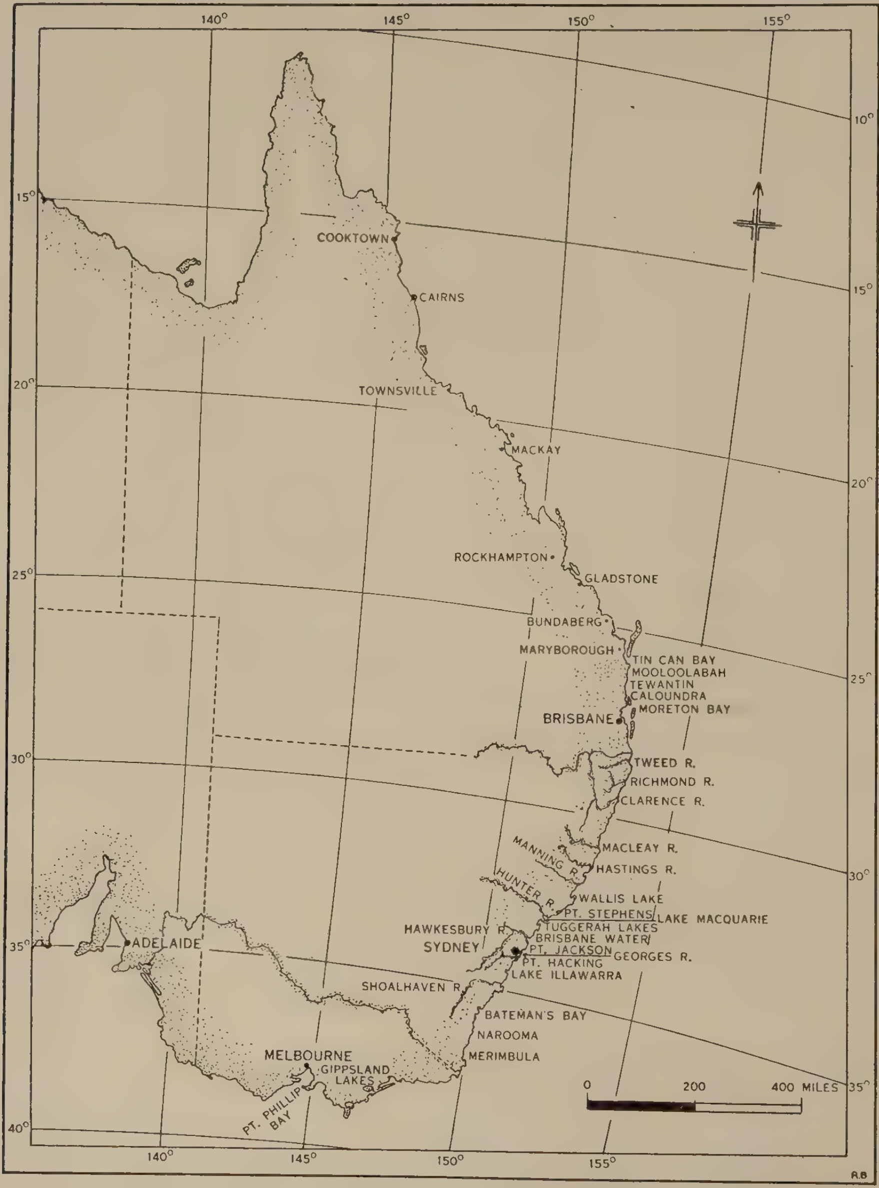
The number of men in the New South Wales fishery was not recorded until 1910. Previously the number fishing in some individual districts had been mentioned in the reports of the district inspectors.

Each year a table is published from the returns of the local inspectors showing the number of men actively fishing. In comparing this with the number of licences issued, it is obvious that many of the licensees did not fish regularly. The intermittent activities of the part-time fishermen proved an annoyance to full-time fishermen on two accounts; firstly, that they were alleged to compete unfairly with regular fishermen as they fished only when fish were plentiful or when activity in their own trade was slack, but, more seriously, that being relatively amateurs they severely harassed the fish, making them wild and scaring them from the fishable grounds. Such fishermen also operated in the week-ends, when the regular fishermen rest the grounds in order to entice the fish back to them. Agitation led to the enforcement in 1946 of a law permitting the issue of fishing licences only to those persons who derived a substantial proportion of their income from personal exertion in the fishing industry.

In the present paper, in assessing the catch per man, the number of men recorded as actually engaged in fishing has been used in the computation rather than the number of men to whom fishing licences have been issued.

In Queensland there has long been divided control of the fishing industry; the administration of fishing activity itself being controlled by the Fisheries Section of the Department of Harbours and Marine, the marketing of fish being at first uncontrolled and operated by various agencies, including cooperatives in different places. However, the Fish Supply Management Act of 1935 placed control of marketing in a Fish Board. At first the activities of the Board were confined to the Brisbane metropolitan fish supply district, between Tweed Heads and Noosa. Since 1944, branch markets and depots have been erected in other areas to the north and now practically every district from the southern border to Cairns comes within the scope of the Board. One of the requirements of the Act is that all fish must be marketed through the depots or markets operated by the Board. As a consequence the catch is very well known for those districts served by the Board. Until 1946 the statistics published by the Board related solely to the receival at the Brisbane market, plus an estimate of the total catch for the State. From 1946 the actual receivals of all the important species are recorded for each fish supply district.

The licensing of fishermen is administered by the Department of Harbours and Marine. Unfortunately the method of recording does not allow differentiation of deep-sea fishermen from the estuarine fishermen, and all the licences issued from Brisbane are grouped together although they cover several different fishing localities scattered along 100 miles of coast. Nor can the full-time fishermen be distinguished from those who take out a licence in order to use a net when on holidays or on a part-time basis. As a result, unless one assumes that a constant proportion of the licences issued each year are issued to full-time fishermen, and therefore that use of the catch per number of men licensed still gives an index of the catch per man actually fishing, no estimate of the catch per man is possible for Queensland. Also, it would not be possible to give the catch per man for each of the fishing places in the Brisbane licensing area. Consequently no attempt will be made in this paper to estimate the catch per man in Queensland waters.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ROCKHAMPTON
GLADSTONE
BUNDABERG
MARYBOROUGH
TIN CAN BAY
MOOLOOLABAH
TEWANTIN
CALOUNDRA
MORETON BAY
BRISBANE
TWEED R.
RICHMOND R.
CLARENCE R.
MACLEAY R.
MANNING R.
HASTINGS R.
HUNTER R.
WALLIS LAKE
PT. STEPHENS
LAKE MACQUARIE
TUGGERAH LAKES
BRISBANE WATER
HAWKESBURY R.
SYDNEY
PT. JACKSON
GEORGES R.
PT. HACKING
LAKE ILLAWARRA
SHOALHAVEN R.
BATEMAN'S BAY
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Fig. 1.—Eastern Australia, showing the important mullet-producing centres.

(*b*) *Total Catch*

The sea mullet (*Mugil cephalus*) of the eastern Australian seaboard (Fig. 1) forms one stock, the local populations of which are regularly mixed by the periodic "hardgut" and spawning migrations (Kesteven 1942). Consequently, in attempting to assess the condition of the fishery it is necessary to consider the stock as a whole, irrespective of State boundaries and of differing State controls.

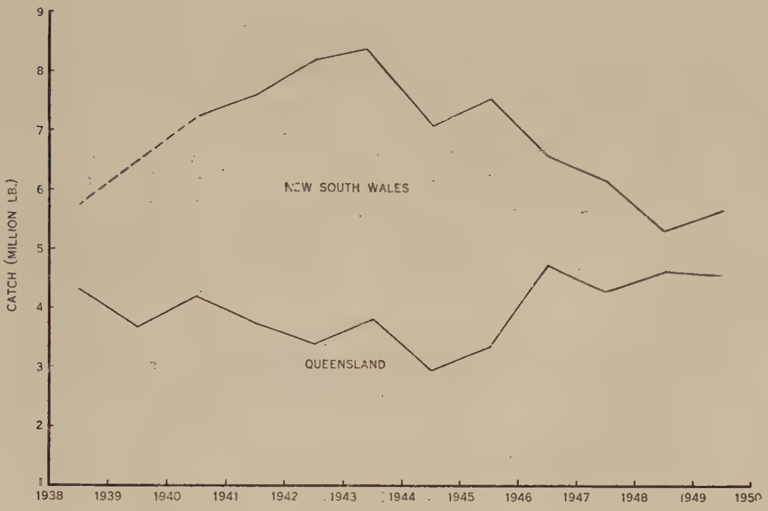

Fig. 2.—Total catch of mullet in New South Wales and Queensland. No record of catch was kept in New South Wales in the year 1939-40.

The annual catch of mullet for eastern Australia during the last 10 years has averaged a little over 11,000,000 lb. (Table 1 and Fig. 2), of which New South Wales provides approximately 7,000,000 lb. and Queensland almost 4,000,000 lb. Victoria's production, only averaging about 71,000 lb., is extremely variable (Fig. 3), and comes entirely from the eastern portion of the State, from just west of Port Phillip Bay to the New South Wales border. The fish are probably best regarded as stragglers or outlying communities of the east coast mullet. Victoria has experienced two large peaks in its mullet catch, one in 1917-19 (Kesteven 1492) and another greater one in 1942-43. Migrant or nomadic stragglers of the eastern stock reach north-eastern Tasmania in small numbers; but they are so few that no separate record is kept of their catch.

The precise northern limit of the stock is uncertain. Kesteven (1942) placed it at Mackay. Commercial catches of the species are made regularly as far north as Gladstone, and often to Rockhampton. The majority of mullet marketed from centres further north are the blue tail, *Mugil delicatus* Alleyne and Macleay.

TABLE 1

MULLET CATCH (LB.) IN THE EASTERN STATES OF AUSTRALIA, INCLUDING THREE SECTIONS OF NEW SOUTH WALES, AND SHOWING THE VARIABILITY AND THE COEFFICIENT OF VARIATION (V) IN EACH AREA

Area	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	Mean	V (%)
Northern N.S.W.*	4,773,440	5,419,164	6,461,287	6,902,816	5,774,990	6,268,427	5,132,869	4,905,228	4,297,878	4,621,330	5,455,743	15.2
Mid N.S.W.	1,368,710	1,309,184	922,082	834,965	906,182	875,368	660,506	757,825	726,465	834,669	919,595	24.3
Southern N.S.W.	1,071,210	792,955	834,823	554,616	435,833	473,504	877,465	540,934	365,139	393,718	634,019	36.3
Total, N.S.W.†	7,292,460	7,626,763	8,226,502	8,303,082	7,117,005	7,617,681	6,623,690	6,210,787	5,378,682	5,749,747	7,014,639	12.9
Queensland‡	4,284,459	3,730,305	3,441,458	3,898,813	2,901,037	3,368,174	4,706,918	4,389,579	4,652,982	4,611,585	3,998,531	14.8
Victoria	36,359	136,005	242,836	52,453	47,759	26,816	28,804	3,312	10,734	3,017	58,809	121
Total, eastern Australia	11,613,278	11,493,073	11,910,796	12,254,348	10,065,801	11,012,671	11,359,412	10,663,678	10,042,398	10,364,349	11,077,980	6.6

* Northern N.S.W., north of Hunter R. to Queensland border; mid N.S.W., from Hunter R. south to Port Hacking; southern N.S.W., south of Port Hacking to the Victorian border.

† Includes catches listed as "other waters" and thus not attributable to the previous sections.

‡ Mullet catch prior to 1946 estimated as same percentage of total Queensland catch as mullet were in Brisbane market receivals.

TABLE 2

MULLET CATCH (LB.) IN THE INDIVIDUAL FISHING DISTRICTS OF NEW SOUTH WALES, SHOWING THE COEFFICIENT OF VARIATION (V)

District	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	Mean	V (%)
Tweed R.	604,030	830,953	637,393	681,307	430,521	478,904	353,529	381,149	384,689	323,774	510,624	31.3
Richmond R.	298,130	360,540	324,770	436,677	525,709	435,030	326,818	485,529	301,347	368,680	386,323	19.6
Clarence R.	1,504,160	1,789,795	2,823,139	2,910,655	2,566,467	2,833,136	2,143,656	2,109,141	1,888,978	1,594,950	2,216,207	18.3
Nambucca R.	234,850	380,555	130,728	237,058	131,657	207,658	119,855	170,095	94,836	116,126	182,341	44.9
Pt. Macquarie	967,750	867,422	997,373	1,000,028	916,815	914,743	889,120	799,197	607,847	748,864	870,915	13.4
Manning R.	358,260	113,065	281,005	538,582	395,845	256,146	264,721	129,734	111,993	106,541	260,589	51.2
Wallis Lake	391,090	480,200	659,429	665,198	582,863	734,619	593,409	522,355	577,812	951,717	615,868	23.6
Pt. Stephens	415,170	546,638	607,450	433,311	225,113	408,191	441,761	308,028	330,376	410,678	412,671	25.4
Hunter R.	2,170	8,137	23,895	26,497	19,630	184,134	71,703	51,081	48,008	46,470	48,172	103.0
Lake Macquarie	304,710	436,170	249,180	141,192	143,633	128,534	94,225	138,934	143,076	150,864	193,064	56.9
Tuggerah Lakes	578,060	638,900	212,412	224,898	303,198	203,807	163,549	225,228	280,080	301,645	313,177	49.2
Brisbane Water	3,850		5,920	21,043	59,589	51,852	17,713	43,584	15,936	3,801	24,809	77.2
Hawkesbury R.	302,470	117,932	265,299	277,753	276,530	185,883	193,912	161,387	154,726	207,533	214,342	27.7
Port Jackson	49,630	40,390	60,177	70,932	31,757	53,314	60,648	27,530	27,319	50,857	48,155	31.7
Georges R.	107,100	46,095	67,319	54,460	63,701	56,677	51,726	96,103	38,316	50,030	63,152	33.1
Port Hacking	20,720	21,560	28,910	17,470	8,744	11,167	7,030	13,978	19,004	23,499	17,208	37.9
Lake Illawarra	195,370	150,780	175,865	64,167	73,411	104,121	289,177	125,431	49,292	89,474	131,408	17.7
Greenwell Point	468,650	378,280	374,321	246,454	153,814	155,713	262,538	208,058	146,553	206,502	260,088	40.6
Bateman's Bay	157,640	115,220	117,955	96,954	76,771	85,572	126,640	84,442	91,131	51,528	100,325	29.4
Narooma	146,650	94,640	62,428	56,395	54,819	62,957	81,064	40,031	31,417	21,279	65,618	50.6
Merimbula	102,900	53,935	107,654	90,666	70,812	65,141	118,046	82,972	40,746	24,935	76,380	36.7

The sea mullet is of paramount importance in the economy of the estuarine fisheries along eastern Australia, accounting for 37-46 per cent. of the catch. The species contributed 40-52 per cent. of the total annual catch in Queensland from 1937 to 1951; and from 35 to 46 per cent. of the New South Wales total catch from 1939 to 1950. Less than 1 per cent. of the Victorian catch is sea mullet.

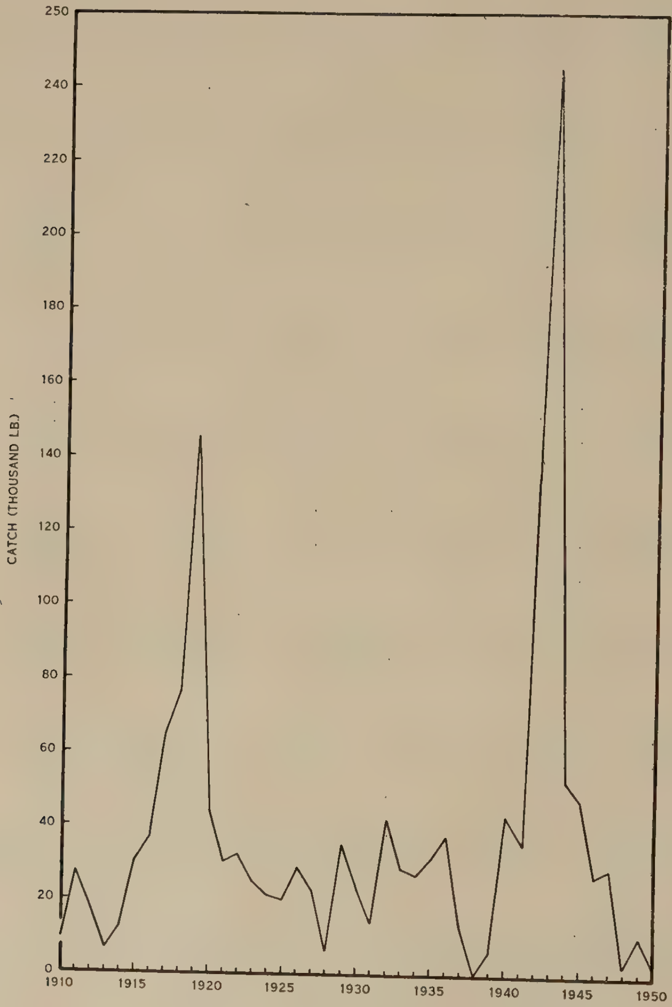

Fig. 3.—Catch of mullet in Victoria, 1910-1950.

From 65 to 83 per cent. of the New South Wales catch of sea mullet came from waters north of Hunter River (Table 1). Including Queensland waters, 66-83 per cent. of the mullet catch comes from north of the Hunter River.

Statistics for each State are published separately, and it is noteworthy that the fluctuations in catch are not necessarily in the same direction for each State in the same year (Table 1). This suggests that variation in population level (or perhaps merely in availability) occurs within the range of the species. Fluctuations in particular waters are even more variable, suggesting that local conditions, rather than factors common to the whole stock generally, determine the level of catch (Tables 2, 3, and 4).

TABLE 3

MULLET CATCH (LB.) IN FISHING DISTRICTS OF QUEENSLAND, SHOWING THE COEFFICIENT OF VARIATION (*V*)

District	1946	1947	1948	1949	1950	1951	Mean	*V* (%)
Brisbane	91,078	61,755	114,175	109,631	175,133	166,247	119,247	25.8
Bundaberg	123,365	236,262	143,290	138,403	161,882	177,956	163,526	17.4
Caloundra	236,184	286,712	292,082	254,736	380,432	202,622	275,801	15.7
Cleveland	173,319	156,386	149,378	116,834	136,391	151,741	147,341	9.2
Coolangatta	470,217	606,467	598,595	463,807	515,040	67,137	453,544	29.4
Coomera	342,504	273,747	189,377	174,771	147,818	139,762	211,331	26.8
Gladstone	47,221	130,508	127,481	106,096	145,152	103,327	109,797	22.2
Maroochydore	56,091	119,588	110,065	189,817	133,648	101,201	118,401	26.1
Maryborough	295,616	525,709	518,192	663,823	747,526	1,123,492	645,726	25.9
Redcliffe	60,237	300,153	211,519	150,794	237,032	64,057	170,632	40.1
Rockhampton	13,928	33,721	33,074	27,453	43,420	36,631	31,341	22.4
Southport	233,163	154,899	156,843	408,127	520,791	366,701	306,754	34.2
Tewantin	477,541	474,686	405,887	607,035	380,751	301,016	441,153	16.7
Tin Can Bay	223,426	155,567	154,372	168,938	194,773	252,006	191,514	14.6
Wynnum	315,405	575,360	500,552	467,349	507,834	406,859	462,226	13.8

Compared with the fluctuations within States or portions of States, the total eastern Australian catch varies little, as is shown by the coefficients of variation (*V*) in Tables 1-3. Generally speaking, variability in numbers is less in the north and greater in the south where the species approaches the limits of its range. (Note, however, that information on Queensland centres is available for only 6 years, whereas that on New South Wales covers 10 years.) This suggests that the fishery is more stable in Queensland and that conditions there are best suited to the mullet.

Over the 10 years considered the trend of the total catch of mullet has been downwards; or at least the mullet catch for the period 1945-1950 has been slightly lower than for the period 1939-1944. However, in the absence of information upon the magnitude of natural fluctuations, it cannot be claimed that a depletionary trend was apparent, particularly without consideration of the numbers of men involved or some other estimate of the effort expended during the periods considered. The overall trend is biased by the trend in New South Wales, where the greatest catch is recorded (Figure 2).

As pointed out above, the catch in individual rivers is more variable than the catch along the whole coast. There is no uniformity in the variation shown by the catch from different rivers (Tables 2 and 3). The

TABLE 4

DISTRICTS RANKED IN ORDER OF IMPORTANCE ACCORDING TO VARIOUS MEASURES

	Total East Coast Catch	State Catch	Catch per Man	Catch per Net
Queensland:				
Rockhampton	33	15		
Gladstone	27	14		
Bundaberg	22	10		
Maryborough	3	1		
Tin Can Bay	19	8		
Tewantin	8	4		
Maroochydore	26	13		
Caloundra	13	6		
Redcliffe	21	9		
Brisbane	25	12		
Wynnum	6	2		
Cleveland	23	11		
Coomera	17	7		
Southport	12	5		
Coolangatta	7	3		
New South Wales:				
Tweed R.	5	4	2	2
Richmond R.	10	6	6	5
Clarence R.	1	1	1	1
Nambucca R.	20	12	8	7
Pt. Macquarie	2	2	3	3
Manning R.	14	8	12	11
Wallis Lake	4	3	4	4
Pt. Stephens	9	5	11	10
Hunter R.	32	19	17	15
Lake Macquarie	18	11	5	6
Tuggerah Lakes	11	7	9	8
Brisbane Water	34	20	19	12
Hawkesbury R.	16	10	7	9
Pt. Jackson	32	18	21	19
Georges R.	31	17	18	18
Pt. Hacking	35	21	20	21
Lake Illawarra	24	13	13	13
Greenwell Point	15	9	10	14
Bateman's Bay	28	14	14	17
Narooma	30	16	15	20
Merimbula	29	15	16	16

TABLE 5

CATCH (LB.) PER MAN AND NUMBER OF MEN IN THE FISHING DISTRICTS OF NEW SOUTH WALES, 1941-1950

District	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950
Tweed R.	9,293	14,838	11,432	10,372	9,359	4,913	5,356	6,049	6,106	5,488
	65	56	47	(102)*	46	(186)*	66	63	63	59
Richmond R.	3,388	3,569	8,405	10,372	8,617	4,913	3,335	5,276	3,863	4,142
	88	101	39	(102)*	61	(186)*	98	92	78	89
Clarence R.	8,745	10,847	16,607	21,884	14,655	12,372	10,159	12,445	12,593	10,850
	172	165	170	133	175	229	211	162	150	147
Nambucca R.	3,350	6,914	2,174	4,159	2,687	3,099	1,517	3,093	4,311	6,451
	70	55	60	57	49	67	79	55	22	18
Pt. Macquarie	10,519	7,478	12,163	8,197	7,903	4,677	5,169	5,549	4,340	8,414
	92	116	82	122	116	137	172	144	117	89
Manning R.	3,010	1,812	2,541	5,475	3,412	2,227	2,941	2,027	2,744	2,478
	119	90	110	99	116	115	90	64	40	43
Wallis Lake	6,518	8,731	9,668	7,735	7,378	5,972	4,987	6,416	7,046	11,896
	60	55	68	86	79	123	119	97	82	80
Pt. Stephens	3,707	4,712	6,825	3,835	1,924	3,459	3,163	2,702	3,933	4,831
	112	116	89	113	117	118	146	114	84	85
Hunter R.	197	406	2,172	1,558	1,308	3,257	1,938	1,309	2,667	2,112
	11	20	11	17	15	(96)*	37	39	18	22
Lake Macquarie	6,094	10,904	6,388	2,956	2,979	3,257	2,546	2,277	3,765	5,388
	50	40	39	48	48	(96)*	37	61	38	28
Tuggerah Lakes	5,898	7,099	2,795	2,585	3,609	2,754	2,210	1,816	4,001	4,845
	98	90	96	87	84	74	79	124	70	62
Brisbane Water	275		348	915	2,383	2,160	984	1,556	1,084	817
	14	14	17	23	25	24	18	28	14	12
Hawkesbury R.	6,172	5,896	4,279	4,273	3,950	2,512	2,056	2,324	4,072	6,289
	49	20	62	65	70	74	70	69	38	33
Pt. Jackson	662	808	746	606	256	360	518	244	536	1,136
	75	50	90	117	124	148	117	113	51	45
Georges R.	1,727	1,048	1,432	1,135	1,179	1,030	1,231	2,084	1,277	2,001
	62	44	47	48	54	55	42	40	30	25
Pt. Hacking	628	458	741	624	336	385	390	998	1,357	2,349
	33	49	39	28	26	29	18	14	14	10
Lake Illawarra	1,480	10,052	3,601	705	807	1,370	3,249	2,023	1,369	2,227
	132	15	43	91	91	76	89	62	36	33
Greenwell Point	3,749	4,150	9,129	3,912	3,662	2,132	3,492	2,972	2,991	3,971
	125	85	41	63	42	73	76	70	49	52
Bateman's Bay	4,148	2,618	4,064	1,795	1,566	1,451	2,435	1,656	2,336	1,610
	38	44	29	54	49	59	52	51	39	32
Narooma	4,583	3,640	2,837	2,256	2,045	1,067	1,724	976	932	989
	32	20	22	25	21	59	47	41	32	21
Merimbula	1,744	2,360	3,987	2,518	874	899	2,270	1,782	1,074	959
	59	23	21	36	81	72	52	40	43	26

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* In 1944 and 1946 the number of men in the Tweed R. and Richmond R. were recorded together as was done for Hunter R. and Lake Macquarie in 1946. The totals of each district were added to obtain the mean.

Clarence River provides the largest mullet catch each year, but more consistent in maintaining their level of catch are Port Macquarie (Hastings River) and Lake Illawarra in New South Wales and some seven rivers in Queensland. (Note, however, that the sampling period for Queensland rivers is less than that for New South Wales so that the comparison may not be just.) In Table 4, the various districts are listed from north to south and ranked according to their importance along the eastern coastline as a whole and according to their importance within each State. The data on men and gear on which this table is based are grouped according to fishing districts (i.e. the administration area patrolled by a fisheries inspector), so that information on individual rivers is not possible.

(c) *Catch per Unit of Effort*

The total catch is a useful index, economically, but has no biological significance unless the effort expended and the types of gear are constant.

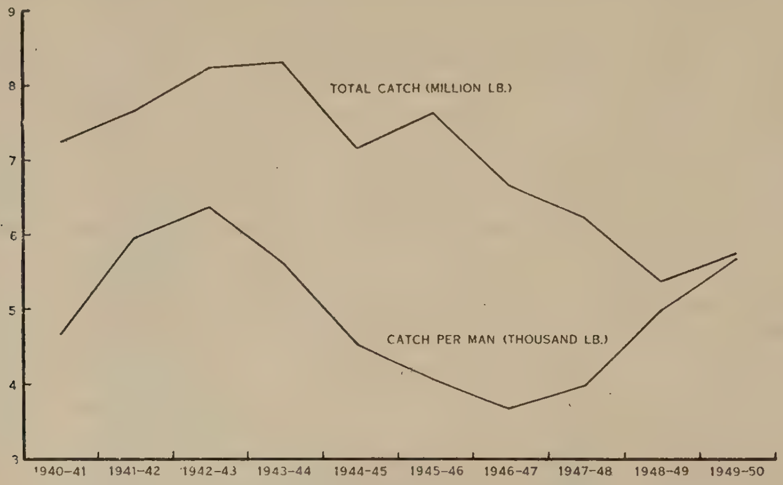

Fig. 4.—Total catch and catch per man of mullet in New South Wales, showing the general parallelism of the trends.

Neither of these parameters is constant from year to year in the Australian fishery. Information on the catch per unit of effort is available only from New South Wales, in whose reports the numbers of men and nets licensed have been recorded since 1941.

The calculated catch per man for various districts is set out in Table 5, and the catch per man for the whole State is shown in Figure 4. Table 4 shows that the Clarence River, besides producing the greatest weight of mullet, also provides the greatest catch per man, followed in this measure by the Tweed River and Port Macquarie. These are all rivers with a large population of fishermen, so that the high catch per man is not the result of only a few fishermen exploiting the area.

TABLE 6

CATCH (LB.) PER NET AND NUMBER OF NETS IN THE FISHING DISTRICTS OF NEW SOUTH WALES, 1941-1950

District	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950
Tweed R.	20,134 30	34,623 24	10,128 (95)*	14,519 (77)*	10,500 41	10,752 (85)*	8,417 42	9,773 39	7,258 53	8,994 36
Richmond R.	5,963 50	13,353 27	10,128 (95)*	14,519 (77)*	10,308 51	10,752 (85)*	4,416 74	8,092 60	4,367 69	6,249 59
Clarence R.	17,490 86	20,747 86	14,977 186	24,449 116	18,871 136	20,832 136	10,718 200	8,112 260	8,665 218	8,663 184
Nambucca R.	13,049 18	22,385 17	4,508 29	8,877 24	2,633 50	8,306 25	2,261 53	2,538 67	2,205 43	3,746 31
Pt. Macquarie	28,463 34	18,857 46	18,469 54	13,699 73	9,452 97	8,095 113	6,787 131	6,343 126	7,894 77	6,346 118
Manning R.	7,025 51	2,626 61	5,590 50	9,974 54	5,997 66	5,227 49	6,016 44	2,948 44	2,799 40	1,746 61
Wallis Lake	13,986 29	13,302 35	15,335 43	13,575 49	14,571 40	11,661 63	7,608 78	7,914 66	8,025 72	12,047 79
Pt. Stephens	4,031 103	4,837 113	8,437 72	5,855 74	3,042 74	5,102 80	5,592 79	5,611 64	5,696 58	3,394 121
Hunter R.	729 3	4,068 2	3,982 6	3,785 7	2,181 9	6,013 (52)*	4,780 15	3,629 13	1,655 29	1,787 26
Lake Macquarie	14,510 21	25,657 17	7,118 35	5,883 24	4,467 32	6,013 (52)*	2,692 35	3,087 45	4,615 31	4,866 27
Tuggerah Lakes	5,780 100	21,297 30	10,120 20	4,016 56	5,414 56	3,996 51	1,686 97	2,322 97	3,183 88	2,900 104
Brisbane Water	481 8	7	1,184 5	3,006 7	2,979 20	17,269 3	1,181 15	3,353 13	1,226 13	7,600 5
Hawkesbury R.	13,151 23	16,848 7	2,793 95	2,222 125	1,947 142	3,645 51	1,199 120	5,206 31	3,516 44	3,052 68
Pt. Jackson	1,909 26	4,039 10	3,144 22	5,066 14	1,984 16	2,423 22	3,567 17	1,196 23	803 34	1,640 31
Georges R.	10,710 10	1,844 25	2,926 23	2,178 25	1,676 38	2,267 25	1,989 26	2,597 37	1,533 25	1,191 42
Pt. Hacking	2,072 10	1,869 11	3,212 9	1,456 12	673 13	1,015 11	1,005 7	1,165 12	1,188 16	783 30
Lake Illawarra	4,543 43	7,936 19	4,038 41	2,069 31	1,412 52	3,155 33	6,153 47	8,689 34	913 54	930 79
Greenwell Point	2,493 188	6,755 56	5,587 67	4,040 67	2,136 72	3,798 41	4,444 59	3,526 59	2,289 64	2,908 71
Batemans Bay	4,777 33	3,032 38	2,741 43	2,620 37	1,968 34	4,504 19	5,506 23	2,413 35	2,604 35	991 52
Narooma	2,993 49	3,380 28	2,312 27	2,256 25	1,768 31	1,249 25	3,845 23	1,143 35	1,496 21	629 33
Merimbula	4,900 21	4,494 12	3,954 27	3,357 27	1,727 41	3,409 19	3,149 35	5,124 16	348 133	1,038 24

* The number of nets used in the Tweed R. and Richmond R. were recorded together 1943, 1944, and 1946. So were the nets for the Hunter R. and Lake Macquarie in 1946. In each case the catches of both places were added and the mean catch attributed to each.

There does not appear to be any obvious trend of increase or decrease in the catch per man either in individual districts (Table 5) or in New South Wales as a whole (Fig. 4). The curve of the catch per man shows the same type of trend as that of the catch, rising to a maximum and declining and then rising again, but the two curves are not in phase and no exact correlation is apparent. For many rivers there is no apparent relation between the catch per man and the number of men; but some, for instance Port Macquarie, show a decline in catch with an increasing number of men. In most cases, the wide variation in catch per man must be based on factors such as availability or population density of fish. In the Clarence River, for example, the catch per man varied during the 10-year period in review from 8,745 lb. to 21,884 lb., and variations of a similar order are apparent in various districts.

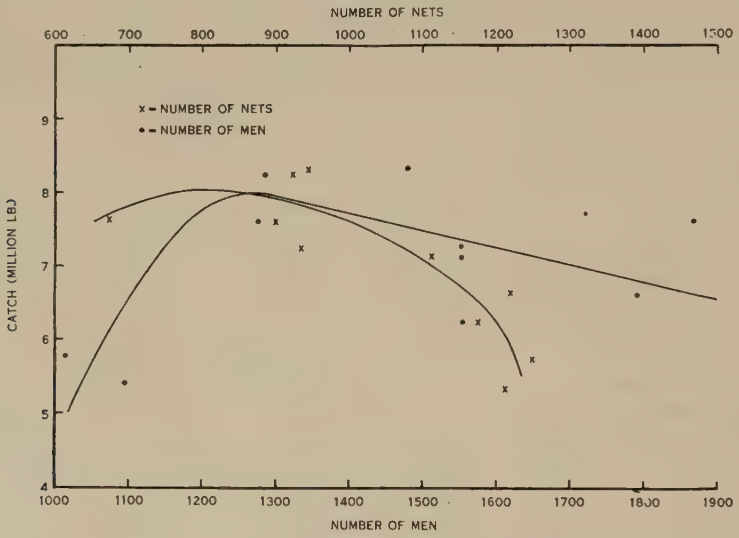

Fig. 5.—Relation between total catch and number of men and between total catch and number of nets, based on data for 1939-1949 in New South Wales.

As with total catch, the variation in catch per man is not in the same direction in different rivers in the same years but is independent within each river system, though the closer the systems are together the more they tend to follow the same course of fluctuations, as can be seen in Tables 5 and 6 where the districts are listed from north to south along the New South Wales coastline.

Another measure of effort, catch per net, is given in Table 6. Both set and hauling nets are counted, there being no way of determining what proportion of the catch is obtained by each type. The picture is similar to that given by the catch per man; variability within a system, no uniformity in fluctuations when one river is compared with another, but the closer the rivers, the more similar the pattern of variation.

The Clarence River, Tweed River, and Port Macquarie provide the highest catches on this measure, as they did with the catch per man. While in general there is no regularity about the relation of catch per net and the number of nets, in other cases the diminished catch per net is shown with an increase in nets.

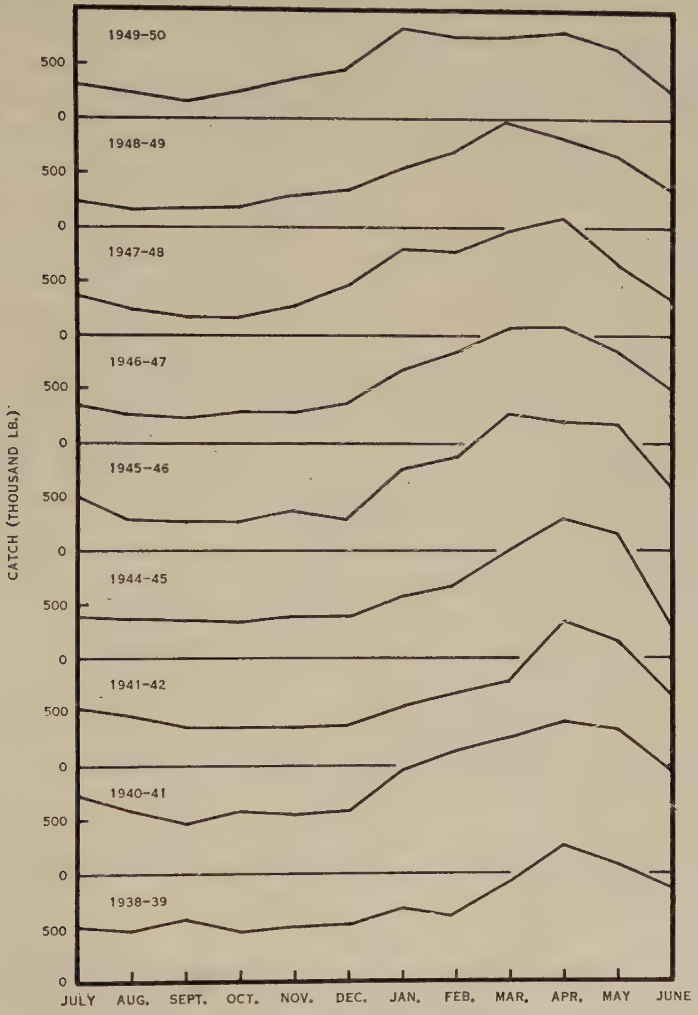

Fig. 6.—Monthly variation in mullet catch in New South Wales, 1938-39 to 1949-50. No data available for 1939-40, 1942-43, and 1943-44.

However, between the number of men and total catch for the whole State, and between the number of nets and total catch there is a suggestion of a curvilinear relation (Fig. 5). These figures suggest that, under the conditions prevailing during the period 1941-1950, the best catch was obtainable when the industry supported 1300 men or 850 nets. This may be a fortuitous result of concurrent changes in population levels or in intensity of fishing, so that it is not possible to claim that this is the optimum intensity of fishing.

III. Seasonal Catch

The catch of mullet is not distributed evenly throughout the year. In New South Wales (Fig. 6) there is a period of low, fairly level catch from July to December; a similar phase extends from August to December in Queensland (Fig. 7). In January in both States the catch first increases normally, and continues to do so until the peak catch is taken in April, or sometimes in March, in New South Wales. In Queensland the peak is usually in May, but the heavy summer rains of southern Queensland sometimes disrupt this pattern, e.g. in 1950-51, so that the peak catch is taken earlier in the summer. After the month of greatest catch, production falls away to the low level by July in New South Wales and by August in Queensland, where the season lasts a month longer.

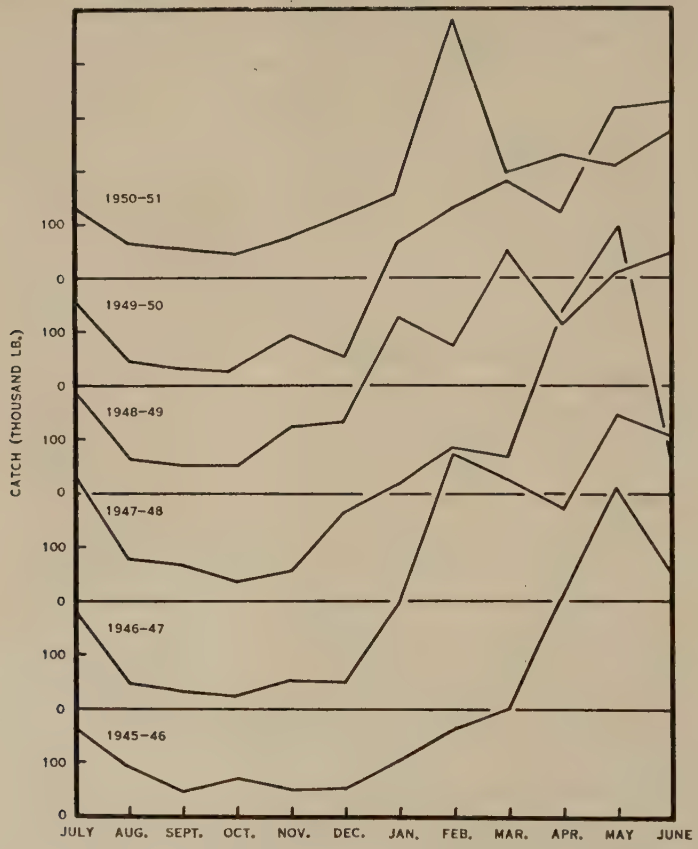

Fig. 7.—Monthly variation in the mullet catch in Queensland, 1945-46 to 1950-51.

There is more variability in the pattern of catch in Queensland, owing, as explained above, to the effects of varying summer rainfall. However, the catch of individual rivers is more variable than is the pattern for the whole coast. Figure 8 shows the monthly catch in the Clarence River. The catch pattern in general is similar to that for the whole of New South Wales, commencing with a period of low catch from late

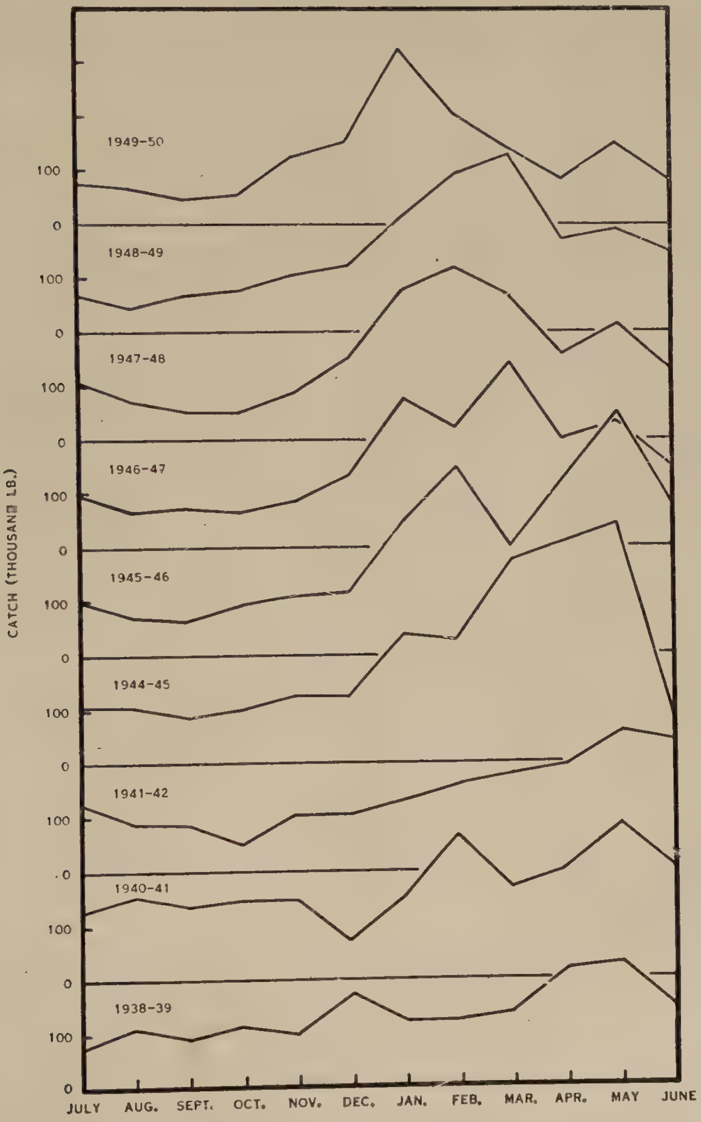

Fig. 8.—Monthly variation in the mullet catch in the Clarence River 1938-39 to 1949-50. No information available for 1939-40, 1942-43, and 1943-44.

winter, followed by increasing catch from midsummer to autumn. But there is far more variability from month to month, and variability in the month in which the greatest catch occurs, than is the case when the catch from the State as a whole is considered.

The biological phenomena connected with the movements and migrations of mullet associated with these patterns of catch have been explained by Kesteven (1942).

IV. COMPOSITION OF CATCH

A system of market measurements of mullet previously provided some information on the size composition of the mullet stocks (Kesteven 1942). War-time exigencies prevented resumption of these measurements until 1945. It is desirable to examine the data taken during the two periods to determine whether any change in the size composition of the marketed stock had taken place.

The collection of these measurements was intended to be made as randomly as possible amongst the market consignments, yet there is undoubtedly room for error in personal bias, conscious or unconscious, in selecting material. From the results it is felt that randomness was achieved with some measure of success in New South Wales, but it is felt by the author, from personal observations of the market consignments, that the Queensland results are consistently biased towards large fish. This may have been due to the relatively fewer measurements made in the Queensland market than in New South Wales. Demands upon the time of the market measurer by other sections of the Division's work led to a virtual cessation of mullet measurements in 1949. This has now been revived (1952) in order to trace the effects of recent regulatory measures in New South Wales.

(*a*) *Annual Catch Composition*

The annual size composition of the mullet catch taken in New South Wales waters for several years and in Queensland for the years 1947-1950 combined are shown in Table 7.

In New South Wales the modal group was 28 cm. in 1940, 1941, 1947, and 1948, but 29 cm. in 1939, 1945, 1946, and 1949. However, the modal group in Queensland appears to be higher at 32 cm. The sea mullet matures at approximately 32 cm. (Kesteven 1942; Thomson 1951), so that most fish caught in New South Wales are still immature and those of Queensland just reaching maturity. The difference could be explained by the fact that the height of the mullet run is reached about a month later in Queensland than in New South Wales, and the growth of the mullet in a month and two weeks would just cover this difference in size (Thomson 1950, Fig. 1).

Until May 11, 1951, the legal minimum length of mullet in New South Wales was 12 in., equivalent to 30.5 cm. total length or 27.1 cm.

TABLE 7

MARKET MEASUREMENTS OF MULLET, NEW SOUTH WALES AND QUEENSLAND

L.C.F. Size (cm.)	New South Wales								Queensland
	1939	1940	1941	1945	1946	1947	1948	1949	1947-1950
Under 20									39
20	5		46	2					12
21	11	3	94			7		2	26
22	16	8	143	21	2	21	1	2	37
23	53	44	234	109	12	35	2	8	54
24	86	180	468	481	107	92	26	20	100
25	151	551	1056	1183	732	544	145	51	138
26	220	1218	2021	2248	2238	1515	474	186	159
27	262	2021	2833	2988	4309	3273	1066	418	220
28	255	2481	3079	3437	5668	4414	1506	526	273
29	281	2095	3063	3753	6297	4401	1407	585	287
30	231	1666	2730	3596	5721	3792	1119	515	375
31	261	1163	2280	3009	4647	2864	800	423	414
32	217	770	2083	2335	3755	1987	467	315	448
33	173	507	1816	1682	2903	1413	351	248	380
34	149	374	1517	1197	2248	1060	226	143	346
35	133	338	1179	870	1740	803	155	90	332
36	123	307	836	639	1393	606	106	56	302
37	109	232	589	411	1042	552	72	57	261
38	89	210	403	299	839	387	63	57	220
39	76	173	322	206	691	315	41	27	195
40	74	122	304	161	496	279	39	14	183
41	32	127	225	142	375	178	47	8	157
42	39	90	156	132	270	118	39	6	109
43	20	80	116	92	168	78	29	5	90
44	20	47	87	71	133	37	25	5	70
45	25	54	61	39	98	27	14	2	54
46	9	62	75	14	82	23	17	3	40
47	7	54	58	17	48	17	12	1	15
48	8	60	45	8	27	20	16	2	8
49	5	35	37	8	11	4	22	—	3
50	4	31	10	2	9	13	11	1	1
51	—	15	9	1	5	3	13	—	—
52	—	6	—	1	4	1	8	—	—
53	—	2	—	5	1	—	3	—	—
54	—	2	—	—	—	2	1	—	—
55	—	—	—	—	—	—	4	—	—
56	—	—	—	—	1	—	2	—	—
57	—	—	—	—	—	—	2	—	—
58	—	—	—	—	—	1	1	—	—
59	—	—	—	—	—	—	1	—	—
60	—	—	—	—	—	1	—	—	—
	3054	15,066	26,900	29,159	46,072	29,888	8363	3778	5348

L.C.F. A minimum length of 14 in. was gazetted in New South Wales in May 1951 and lasted until November 2, 1951. Concurrently the mesh of permissible nets was raised from 3 in. to 3¼ in. However, allowances were made during this period so that the nets of the old mesh could be used up in order to prevent hardship upon the fishermen. Subsequently the length became 13 in. from November 2, 1951, to March 20, 1952, when the 14 in. length came into force. It is the expressed intention of the State Department to regulate each year so that 14 in. is the minimum legal length from March 1 until June 30; 13 in. to be the length from July 1 until February 28.

TABLE 8

MULLET SIZE-GROUPS ASSEMBLED TO SHOW THE PROPORTIONS IN RELATION TO THE OLD (PRE-1951) AND NEW SIZE REGULATIONS

Year	Under 12 in. (%)	12–13 in. (%)	13–14 in. (%)	Over 14 in. (%)
New South Wales:				
1939	17.9	16.9	21.5	43.7
1940	13.3	29.9	28.5	28.3
1941	14.6	21.9	25.8	37.7
1945	13.8	22.0	30.1	33.1
1946	6.7	21.6	31.1	40.6
1947	7.7	25.7	33.3	33.3
1948	7.8	29.3	36.3	26.6
1949	7.1	25.0	34.6	33.3
Queensland:				
1947–50	10.6	9.2	16.2	64.0

Until 1951 the regulations in Queensland prescribed a minimum length of 11 in., except for the months of March, April, and May when a minimum of 12 in. was enforced. The period during which the 12 in. minimum was legal was increased in 1951 to cover the months from February to June inclusive.

Kesteven (1942) has already pointed out that a considerable proportion of undersized mullet are marketed. (However, it should be noted that the position of the line marking the minimum legal length is inaccurately placed in his Fig. 21 (d) and (e), as the sizes there are given in terms of L.C.F. and the L.C.F. corresponding to 12 in. total length is 27.1 cm., not 30 cm. as shown.)

An examination of the size distribution shows a not inconsiderable proportion of mullet under the legal size reaching the market (Table 8). However, the number of undersized fish was cut approximately by half after 1945. As can be seen in Table 7 most of these undersized fish were within a centimetre or two of the legal length, but some were as much as 7 cm. under. The mean size at first maturity is 13 in. total length (29.3 cm. L.C.F.). Except in 1940, over 60 per cent. of the mullet marketed exceeded this length. The proportions in these larger size categories are somewhat variable, and the much greater proportion of large fish in the Queensland catch (despite the lower minimum length) should be noted. It should be emphasized that these size intervals relate only to the legal minima and are not year-class intervals, which will be discussed subsequently when considering the seasonal catch composition.

TABLE 9

SIZE COMPOSITION OF COMMERCIAL CATCH OF MULLET IN NEW SOUTH WALES AND QUEENSLAND FOR EACH MONTH EXPRESSED AS PERCENTAGES

Monthly values as the mean for years 1939-1941 and 1945-1949 in New South Wales and for 1947-1950 for Queensland

Size	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
New South Wales:												
Under 12 in.	10.9	5.1	4.2	4.1	3.8	7.7	16.1	9.8	6.9	5.1	10.6	18.8
12-13 in.	29.5	24.6	12.4	15.9	17.3	35.8	38.3	29.0	20.6	32.0	36.0	20.7
13-14 in.	45.3	60.0	45.3	26.5	36.2	46.4	38.3	44.3	42.4	46.5	26.1	31.9
Over 14 in.	14.8	20.3	38.1	53.5	42.7	10.1	7.3	16.4	30.1	17.4	27.3	28.6
Queensland:												
12-13 in.	19.9	9.5	2.2	1.0	12.3	2.7	3.9	3.3	15.1	19.3	14.5	10.9
Under 12 in.	38.0	20.8	6.8	0	12.8	3.3	1.0	1.7	15.9	12.6	27.1	14.3
13-14 in.	14.4	16.2	11.0	17.5	21.0	10.0	19.5	5.3	22.0	18.8	18.6	18.6
Over 14 in.	27.7	46.5	80.0	81.5	53.9	84.0	75.6	89.7	47.0	38.3	39.8	56.2

(*b*) *Seasonal Catch Composition*

The size composition of the annual catch gives a picture of the frequency with which fish of different sizes occur in the market, but it reveals nothing of the distribution in time through the year. Whether fish of all sizes are taken uniformly throughout the year or whether certain size-groups are numerous only at certain periods can be ascertained from the monthly catch composition figures (Table 9). It can be seen from these figures that in New South Wales the proportion of undersized fish consigned to market tends to increase during the period July to November, when the large fish over 14 in. are poorly represented in the catch. The 12-13 in. group are most poorly represented in the catch during March and April and best in June and July. This temporal distribution is probably due to the almost complete growth past the 12-13 in. size by the small III+ fish by the end of February, and the failure of the large II+ fish to enter this size-group in any significant quantity until May.

The fish in the 13-14 in. group are well represented throughout the year, but are most important in the months of June and July. Fish of a size greater than 14 in. are few from July to January but then become increasingly common in the catch, being in their greatest concentration from March to May.

The Queensland figures are more open to suspicion than those from New South Wales. As so few fish were taken in the monthly samples, the results of all years have been combined to give the monthly results shown in Table 9. Fish under 12 in. were most commonly marketed from September to February. It should be remembered that during the years when sampling took place the legal minimum length in Queensland from June 1 until February 28 was 11 in. The proportions under this limit were as follows: September 2.9 per cent., November 8.5 per cent., December 1 per cent., January 13.5 per cent., February 8.2 per cent. The 12-13 in. group were practically non-existent in the Queensland catch during March and April (as in New South Wales), but otherwise formed practically the same proportion of the catch through the year. The 13-14 in. group were fewest from June to August, but otherwise were equally represented throughout the year. Fish of 14 in. and over were commonest in the catches from March to August; the season lasting longer than in New South Wales. South Wales.

TABLE 10

AGE COMPOSITION OF COMMERCIAL CATCH OF MULLET IN NEW SOUTH WALES EXPRESSED AS PERCENTAGES OF TOTAL

IV+ and older fish grouped together

Year	Age	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1939	II+	67.3	53.0	41.4	42.1	52.5	44.0	28.3	82.7	98.2		72.8	71.0
	III+	32.7	44.7	49.8	43.5	47.5	53.2	67.8	17.3	1.8		26.9	29.0
	IV+		2.3	8.8	14.4		2.8	4.9				0.3	
1940	II+	0.4	25.8	13.6	32.7	41.7	81.1	61.0	57.5	78.8		65.6	30.5
	III+	96.8	73.8	85.3	57.9	48.7	18.9	39.0	42.5	21.2		34.4	69.5
	IV+	2.8	0.4	1.1	9.4	9.6							
1941	II+	57.5	46.5	28.6	25.8	34.4	55.4	30.5	37.5	40.6	35.3	43.2	27.0
	III+	41.8	53.4	68.7	65.4	59.2	44.6	68.8	59.6	59.0	64.2	54.7	71.1
	IV+	0.7	0.1	2.7	5.8	6.4		0.7	2.9	0.4	0.5	2.1	1.9
1945	II+					27.7	35.6	43.4	35.5	36.0	47.8	38.8	32.0
	III+					63.7	63.0	56.5	64.4	63.9	52.1	60.8	67.1
	IV+					8.6	1.4	0.1	0.1	0.1	0.1	0.4	0.9
1946	II+	26.1	27.3	17.2	12.0	19.8	39.8	40.0	42.0	38.3	41.8	32.5	45.4
	III+	73.1	71.9	77.6	75.8	70.5	59.3	59.9	57.9	61.6	58.1	67.4	54.5
	IV+	0.8	0.8	5.2	12.2	9.7	0.9	0.1	0.1	0.1	0.1	0.1	0.1
1947	II+	40.2	29.7	21.6	20.0	21.1	43.0	54.4	38.8	27.5	37.1	46.6	39.5
	III+	59.7	70.2	76.0	68.3	68.5	55.7	45.5	61.1	72.4	62.8	52.2	54.9
	IV+	0.1	0.1	2.4	11.7	10.4	1.3	0.1	0.1	0.1	0.1	1.2	5.6
1948	II+	37.0	24.5	11.1		33.4	64.3	47.9	59.5	58.2	37.2	43.6	33.2
	III+	62.9	75.4	47.9		63.0	35.7	48.5	40.5	41.8	62.8	56.4	66.8
	IV+	0.1	0.1	41.0		3.6		3.6					
1949	II+	22.5	41.6	31.9		21.0	56.8	50.0	34.4	74.0			15.6
	III+	77.4	58.3	68.0		66.3	43.2	50.0	65.6	26.0			84.4
	IV+	0.1	0.1	0.1		12.7							

As mentioned when discussing the annual catch composition, these figures relate to the legal size limits only. In Table 10 the age distribution of the catch from month to month is shown. All age-groups of IV+ and older are grouped together, because the V+ and older groups are negligible in their representation (see also Kesteven 1942, Table 7). Owing to the legal minimum length being part way through the size range of II+ fish this age-group is not as well represented in most months as the III+ fish, which form the bulk of the catch. IV+ and older fish form any considerable proportion of the catch only during late summer and autumn. This age-group is poorly represented in the catches from July to December. The absence of these large fish from the records for 1948 and 1949 is probably due to inadequate sampling, as fewer fish (8,000 and 3,700 as against 29,000-46,000) were measured in these years than in the earlier years.

TABLE 11

AGE COMPOSITION OF MONTHLY COMMERCIAL CATCH OF MULLET IN QUEENSLAND, 1947-50 – PERCENTAGES OF TOTAL

Age	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
II+	39.4	21.5	7.0		25.1	6.0	4.0	5.0	28.1	31.9	33.1	22.2
III+	54.0	66.6	82.9	79.5	74.5	71.4	67.2	52.6	60.2	68.1	61.7	60.8
IV+	6.6	11.9	10.2	20.5	0.4	22.6	28.8	42.4	11.7		5.2	17.0

The Queensland figures show a somewhat different picture, but as the sample numbers were much less it is possible that there was a bias towards measuring large fish in this sampling (Table 11).

The proportion of IV+ mullet in the Queensland catch would appear to be higher than in New South Wales, but the number of V+ and older fish is still negligible. As in New South Wales the older fish are taken more plentifully in the migration months, which last till later in the year (July-August) than in New South Wales. It will be noted that in correlation with the lower legal minimum length (11 in.) from August to January inclusive, the proportion of II+ fish in the catch is higher than in New South Wales.

V. CONDITION OF THE FISHERY

The annual and seasonal fluctuations in the catch and in the catch composition having been described, it is now possible to enquire to what extent these figures throw light on the condition of the fishery and to consider what methods of control are needed to give the greatest benefit.

(*a*) *Correlation of Total Catch and Mullet Catch*

Kesteven (1942) has shown that the total estuarine catch in New South Wales has passed through successive phases of increase and decline. His interpretation was that the total catch curve also indicated the trend of catch of mullet because "It is assumed that if for any locality or for the whole State, it can be shown (*a*) that the species composition of the catch has remained fairly constant, and (*b*) that mullet figures largely in the catch, then the data in such cases can be used in an estimate of the condition of the mullet stocks." While his evidence to support his conditions (*a*) and (*b*) were meagre, the facts as shown by the 10 years' catch figures now available confirm the probability that these conditions hold (Table 12). In this table are given not only the figures of the catch for New South Wales, but also those of the catch for the Hastings River, as this is the only case in which data on mullet are available for any period prior to 1939. The coefficient of correlation between the catch of all species and that of mullet is very good, that for all New South Wales being better than that for the Hastings River, as might be expected from Section II, where it was shown that the catches of mullet from a particular river were considerably more variable than from the State as a whole. The correlation is not exact, nor is the fluctuation in total catch equal to the fluctuation in mullet numbers. In all years but 1943, the variation in the total catch from the preceding year was markedly larger than the change in the quantity of mullet. In other words, stocks of other fish also fluctuated in the same way as the mullet in these years.

TABLE 12

CORRELATION OF THE CATCH OF MULLET WITH THE CATCH OF ALL ESTUARINE SPECIES FROM (*a*) HASTINGS RIVER, AND (*b*) NEW SOUTH WALES

Year	(*a*)			(*b*)		
	Mullet (%)	Mullet (lb.)	Total (lb.)	Mullet (%)	Mullet (lb.)	Total (lb.)
1905	40	72,660	176,988			
1906	34	61,908	182,028			
1907	34	194,796	457,884			
1908	43	167,580	401,856			
1909	42	129,444	358,596			
1910	40	155,400	387,492			
1939	45	174,535	360,745			
1941	39	203,980	519,190	42	7,292,460	17,203,200
1942	43	240,624	559,473	41	7,626,763	18,774,684
1943	51	214,876	424,990	43	8,226,502	19,133,518
1944	51	250,834	494,990	39	8,303,082	21,133,518
1945	45	170,040	386,441	36	7,117,065	19,792,288
1946	45	150,632	336,441	43	7,617,681	17,677,723
1947	47	191,050	413,317	41	6,623,690	16,176,838
1948	33	134,683	407,000	40	6,210,787	15,502,327
1949	51	138,128	269,876	46	5,378,682	12,544,783
1950	61	181,352	294,060	49	5,749,747	11,659,181
		$r = 0.88$		$r = 0.92$		

It might be argued that conditions that produce a favourable or unfavourable fluctuation in population numbers of one species would produce similar fluctuations in other species. As all the factors influencing the population numbers are unknown this may be so, but the feeding and breeding habits of the various estuarine species are so varied (Roughley 1951; MacInnes 1950) that such an argument is unconvincing. An alternative suggestion is that the availability of the different species was good or bad in the same year, either through favourable or unfavourable weather for fishing or by reason of movement of the fish onto or from fishable grounds. No records of the mullet catch from New South Wales waters exists for the period 1910-1938. Whether the mullet catch throughout this period formed the same percentage of the total catch as during the last 10 years is unknown. Certainly the data for the Hastings River suggest that it may well be so. However, it is possible that at different periods the mullet catch has had differing temporarily stabilized relations with the total catch, as for the Swan River in Western Australia (Thomson 1950), though here special conditions existed to bring about the effect. There is no evidence against the belief that the mullet catch has been correlated with the total catch in a straight-line relation, and what evidence exists supports it, at least from 1905.

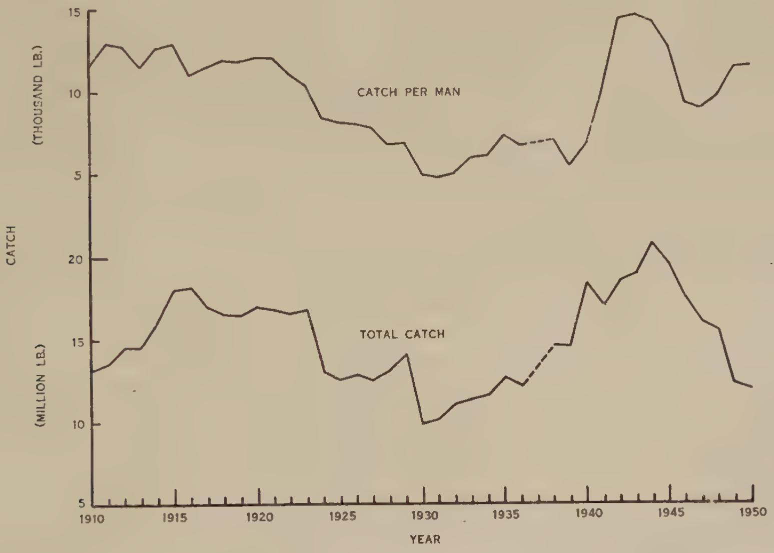

Fig. 9.—Total catch and catch per man in New South Wales estuaries 1910-1950.

(*b*) *Trends in Catch*

The estuarine catch in New South Wales increased from the beginnings of the fishery to a peak in 1915 (Fig. 9), after which the fishery was fairly stable until 1924 when a spectacular drop in catch occurred. The fishery stabilized at a new level for a few years until 1930 when another drop in catch was recorded. The fishery then showed signs of recovery which were accelerated by 1938, and from 1940 to 1948 the catches reached the level of the 1914-1923 period and indeed exceeded the record catch taken in 1915.

In terms of the catch per man the fishery was stable from 1910, when figures of the number of men were first recorded, till 1915, after which there was a drop to a stable phase which lasted till 1922 when the catch per man declined with minor fluctuations to 1931. After this a fairly stable period lasted until 1941, when the catch per man rose sharply, and in the immediately ensuing years rose to values greater than those achieved in the 1910-1921 period.

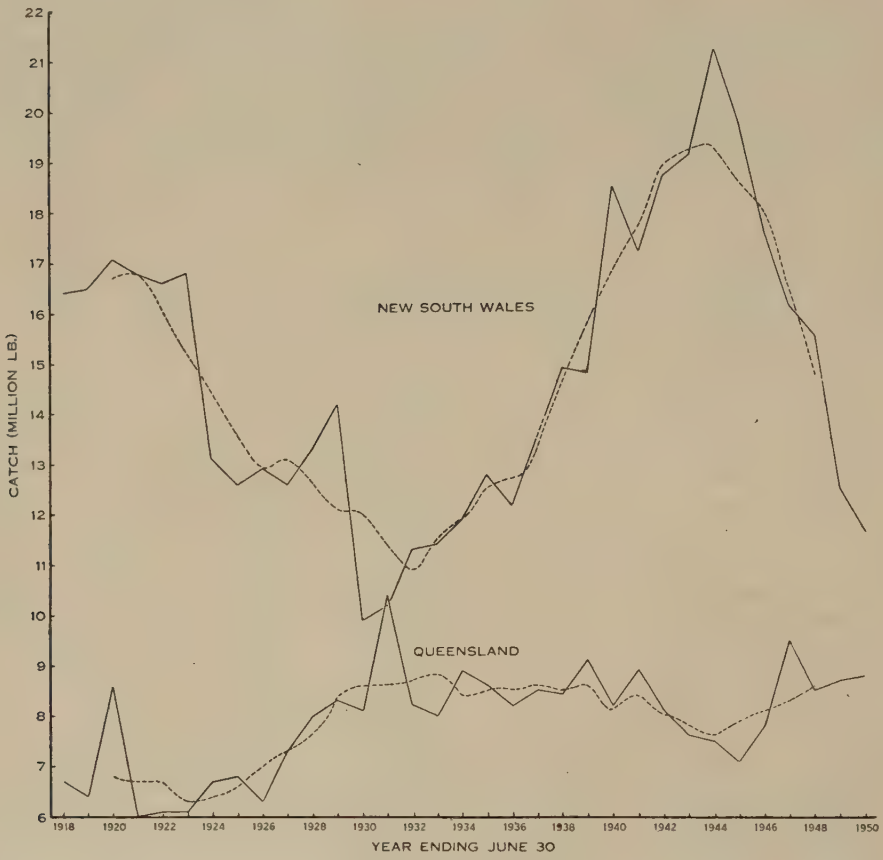

Fig. 10.—Total catch and trend curves (5-year moving average) for New South Wales and Queensland.

In Queensland the estuarine catch has fluctuated about a steady level since 1930, the exception being a period of decline at the beginning of the 1939-45 War when manpower shortage and restriction of areas permitted to be fished caused a drop in the catch. When the curves of catch for the two States are compared (Fig. 10), it appears that, despite irregularities in the year-by-year changes in catch, the secular trends are cyclical and to some extent inverse. The two trend curves are not in perfect phase nor is the amplitude of the curves similar, the number of men fishing and the level of catch being lower in Queensland, hence the absolute variations are also less. This suggests that the curves of catch for mullet given in Figure 2 represent half periods in cyclical curves of catch. There does not appear to be any close relation between the catches in the two States, the index of correlation, *r*, being — 0.30.

(*c*) *Interpretation of the Catch Curves*

The catch curves, as described above, show a period of increasing catches followed by a stable period which passes into a phase of declining catches. Later still an increase in catch occurred once more, but during the last few years signs of a decline are once again evident.

(i) *A Theory of Depletion.*—Kesteven (1942) examined the fishery to the stage reached in 1938, i.e. almost to the end of the period of decline. His conclusion (p. 83) was that depletion existed owing to overfishing. This was a justifiable interpretation of the meaning of the curves of catch, catch per man, and catch per unit of gear in the light of the then current theory of fisheries exploitation advocated by such authors as Russell (1931, 1942), Hjort, Jahn, and Ottestad (1933), Thompson and Bell (1934), and Graham (1935). One or two of the reasons on which Kesteven reached his conclusions were based on slender evidence. The decline in catch, catch per man, and catch per unit of gear were definite, as was the fact that a considerable proportion of the fish taken were immature. But the evidence of decline in yield per man-hour, or of the fact that "both mean length of the total catches and mean length of life are considerably reduced on what they could be" is meagre and largely assumptive. The consequential conclusion "that the fishing rate, coupled with natural mortality, is quite out of proportion to the recruitment ability of the stocks" makes assumptions concerning each of the factors, fishing rate, natural mortality, and recruitment ability, that may be inferred if the interpretation of the meaning of the catch curve is correct but for which there are no data in confirmation.

This theory that the decline in catch was due to overfishing may perhaps be supported by the fact that the period of decline was coincident with an increase in the number of men fishing and with a decrease in the catch per man. During the period of increased catches during 1940-1950 the number of men dropped and the catch per man rose, suggesting that a lessened intensity of fishing had produced greater catches per man and greater catches. However, although this picture fits in very well with the theories of overfishing and of optimum catch, there are alternative explanations for these relations of catch and men which will be discussed in Section V (*c*) (iii).

The term "depletion" itself has been used in different senses by various authors. Huntsman (1948) disdains the term depletion as meaning in origin a condition less than full and thus having indefinite gradations as well as a large number of meanings. He suggested 11 different conditions of reduced catches which may be confused under the variously used terms "depletion" and "overfishing". None of the conditions described by him are duplicated entirely by the facts of the mullet fluctuations.

Kesteven (1942) did not define what he meant by depletion, but in a later paper (1946) he defined it by a list of symptoms, " . . . the stock . . . has become sparser, the density of stock per unit area has fallen; the reproductive and growing potentials of the stock are impaired because (for the present purpose) of the operations of the fishery." Kesteven (1946, p. 101) recognized grades and kinds of depletion. This is the usage of other writers who use the term depletion to signify a condition of reduction in stocks which, besides other factors, can be produced by overfishing (e.g. Russell 1931, 1942; Graham 1935). Others would restrict the term as far as fisheries terminology goes entirely to "reduction, through overfishing, in the level of abundance of the exploitable section of a stock that prevents the full realization of the maximum productive capacity" (van Oosten 1949).

In van Oosten's definition a stable fishery can still be "depleted" (van Oosten 1949, p. 287), and this has been recognized in the conception of the "optimum catch" (Hjort, Jahn, and Ottestad 1933). But other authors have used the term depletion as though it implied a continuing trend of diminishing returns (e.g. Kesteven (1942, 1946) and Blackburn (1949) who, in defining depletion, says, "fish may become more or less continuously scarcer over a considerable period". However, the latter author in dealing with the overfishing of the whitebait *Lovettia seali* Johnston (Blackburn 1950) recognized that "a balance, though not the best balance can be restored if the rate of overfishing is stabilized").

Van Oosten (1949) has carefully distinguished between the condition (depletion), its cause (overfishing), and its symptoms. Others have used the terms depletion and overfishing almost as synonyms (e.g. Van Cleve 1945). Van Cleve (1945) complicates the matter by suggesting that "in one sense . . . overfishing and its copartner depletion may be thought of as economic in nature, and might be defined as that state of a fishery where the abundance of a species upon which it depends has decreased as a result of fishing beyond the point at which the catch per unit of effort is sufficient to permit the boats to operate at a profit." But Burkenroad (1951) has already pointed out that an almost exhausted fishery can still be profitable if the prices are high and methods cheap, so that the biological sense of depletion has no relation to the economic sense suggested by Van Cleve. Kesteven (1946, p. 102) also tended to unite the economic phenomena with the biological in assessing depletion. It is suggested here that the phenomenon of depletion in the sense defined by van Oosten is entirely biological and should be restricted to this sense, although some of the symptoms by which depletion may be recognized, e.g. decline in yield per unit of effort, may also have economic implications.

It should be recalled that most definitions of depletion refer to it as a condition of the stocks, and as such depletion must influence, but is not the same as, the condition of the fishery. A depleted stock may still form the basis of a flourishing industry, particularly if it is stabilized or only slowly declining. Contrarily, if there is no demand, a fishery may be uneconomic or even close down, although stocks may be abundant.

In interpreting the curves of catch and of catch per man, it is therefore necessary to discriminate between the evidence which these curves provide on the abundance of the stocks and that on the state of the fishery. The figures of catch and catch per man obviously are descriptive of the fishery in terms of yield and, when related to prices, in terms of monetary value. But what their relation may be to the abundance of the stocks is debatable.

The catch per unit of effort has been taken as an index of the abundance of stocks (see for instance Ricker (1940), Russell (1942), and Schuck (1949)). But both Huntsman (1948) and Needler (1948) have claimed that it has never been satisfactorily demonstrated that the catch per unit of effort is directly proportional to the population. The index is directly a measure of availability providing fishing intensity does not vary greatly. Fisheries biology has yet to show in any case what the exact relation between availability and true abundance of population might be. It is quite possible for some accident of migration or environmentally stimulated movement to cause a stock of fewer fish to make a greater number available to a fishery than a larger stock which is unfishable.

Schuck (1949) recognized that his population size was in reality an index of abundance without any determinable relation to absolute population size, but he made no recognition of the decline in usefulness of the catch per unit of effort as a measure of abundance as fishing intensity increases (Needler 1948).

The only estimate of catch per unit of effort available in the eastern Australian mullet fishery is the catch per man in New South Wales. The catch per man is comparable year by year only if the time spent in fishing and the gear used are similar year after year. Despite minor modifications in equipment and changes in regulatory requirements concerning length, meshes, etc., the gear used in the fishery has varied very little. There is no estimate of the time expended in the fishery. But is is likely that at various periods, in correlation with varying economic incentive, the time expended in fishing by each man has varied widely.

Assuming, firstly, that fish are equally available each year, and secondly, that the index catch per man is a reasonable representation of the abundance of fish, the curves of catch and of catch per man could be interpreted in the light of the depletion theory to mean that the fishery was expanding up to 1914, and stabilized from then until 1924 when a sharp decline in abundance occurred owing to the increased number of men fishing from 1923 onwards. The fishery was depleted but stable until 1930 when a further increase in fishermen, dating from 1928, forced a further diminution in the stock. In 1941 the catch per man recovered when the number of men decreased, but fell away again in 1946 and 1947 when the numbers increased once more and included many inexperienced ex-servicemen trying to find a place in the industry. At the same time the increased intensity of fishing once more started a depletionary trend in the stock.

(ii) *A Theory of Population Fluctuations.*—That the major fluctuations in fish abundance are attributable to fluctuating environmental factors rather than to effects of fishing activity has been asserted by several authorities in recent years, notably Burkenroad (1948) and Langlois (1948). Recognition that factors other than fishing intensity play their part in the fluctuations of fish stocks is implicit in the writings of many of those dealing with the overfishing problem; for example, in the work of Thompson (1930*a*, 1930*b*) on brood strengths, and in the more general approaches of Russell (1942) and Kesteven (1946). But Langlois asserts that major fluctuations are due to "natural" fluctuations and not to the effects of fishing.

Merriman (1949) has observed that in fisheries with large numbers of eggs the fluctuations in abundance are likely to be due rather to the environment than to the size of the stock. The mullet fecundity is high (Kesteven 1942), so that on this view it would take a severe diminution of breeding stock to decrease the spawning potential sufficiently to lessen the mullet population. It is doubtful whether the mullet fishery is very intense (see Section VI). It would therefore seem likely that the fluctuations in catch observed may be due to "natural" causes (for an alternative explanation see Section V (*c*) (iii)).

If it could be assumed that the effort expended by each man in each year were approximately the same, and if further it be assumed that the availability of fish were equal each year, then the catch curves could be interpreted in the light of the population fluctuation theory as follows. After a period of stable though oscillating population level from 1910 to 1923, a sharp drop in the stock occurred in 1924 (equivalent perhaps to the catastrophic decline of Elton (1942)), followed by another equilibrium period which ended with another fall in 1930. The population cycle changed direction from then, slowly building up till it accelerated in the early 1940's to a peak at which it remained in fluctuating equilibrium until it showed signs of falling once more towards the end of the period.

(iii) *A Theory of Socio-economic Influences.*—Although it is not the function of fisheries biology to initiate or evaluate economic or social trends or to justify political legislation, yet it is necessary in surveying the history of a fishery to examine what part such factors may have played. Garstang (1900) and Kyle (1928), amongst others, gave warning that fish production was not a simple matter of evaluating abundance by means of the catch per unit of effort. Allowance must be made for different intensities of fishing, for changes in gear, and particularly for economic incentive.

The methods used in the fishery have been substantially the same during the period 1910-1950. The legal lengths of nets permissible in certain waters has changed from time to time, but this has had little more than local significance. The factor of intensity of fishing is rather difficult, if not impossible, to assess. The mere number of licences issued is not equivalent to intensity, nor necessarily is the number of men actually fishing. In the absence of information on the time expended on fishing activities little can be decided on this matter. However, some qualitative aspects of the effects of intensity of fishing will be mentioned in discussing economic incentives.

The estuarine fishery catch in New South Wales rose to a maximum in 1915, but then a slight decline set in until 1924 when there was a sharp drop in the catch. After that the fishery was stable for a few years. In June 1915 the New South Wales Government commenced trawling on a commercial basis for the first time. Concurrently with this development the estuarine catch started to decline. Towards the end of 1922 the Government ceased trawling operations (Herlihy 1927; Fairbridge 1948); but in August 1923 the trawling industry recommenced under private enterprise, and in the subsequent season the estuarine catch dropped by 3,000,000 to the new level that was maintained for some years. That it was competition from the trawling industry that produced this decline is borne out by the contemporary reports (Wood 1927, 1928, 1929). No suggestion is made in these reports that mullet were less abundant; on the contrary, it is specifically stated that fishermen deliberately refrained from catching fish during the mullet run because there was no market for the fish. From 1924 to 1940, the estuarine fishery remained at a low level except for a slight increase in the late 1930's. At the end of 1939 the steam trawlers were taken over by the Govrnment for war-time duties (Fairbridge 1952). Freed from much of the competition, the estuarine catch immediately rose despite the lowered manpower consequent upon military commitments. Most of the Danish seine fleet was taken over at the end of 1941, and the estuarine catch rose to a new peak in 1944. In 1945 both trawlers and Danish seiners recommenced fishing (Fairbridge 1952), and from then on the New South Wales estuarine catch declined (Table 13).

Besides competition from the trawling industry the estuarine catch had to compete with low-priced imported fish, a fact often commented upon in the Annual Reports of the New South Wales Fisheries Department. In Table 13 it can be seen that with the establishment of the Government trawling industry imports of fish dropped to a new level. However, in 1923, during the period of transfer of the trawling industry

TABLE 13

EFFECT ON ESTUARINE FISHERIES OF THE TRAWLING INDUSTRY AND OF IMPORTS IN NEW SOUTH WALES

Year	Estuarine Catch (lb.)	Trawler Catch (lb.)	Imports of Fish into N.S.W. (lb.)
1910	13,325,172		7,042,036
1911	13,858,992		7,954,564
1912	14,527,884		9,506,214
1913	14,702,352		9,451,835
1914	16,237,788		9,198,831
1915	18,240,600		10,579,740
1916	18,189,696	1,630,380	10,126,383
1917	17,037,468	1,637,070	8,336,201
1918	16,498,860	1,897,650	8,820,249
1919	16,546,908	3,023,640	5,582,413
1920	17,143,980	5,585,160	8,660,515
1921	16,836,624	5,527,140	7,221,614
1922	16,669,968	5,404,680	8,642,427
1923	16,864,958	2,867,200*	11,302,407
1924	13,147,346	4,813,760	12,412,675
1925	12,645,498	6,316,590	11,949,710
1926	12,996,318	8,461,600	13,512,244
1927	12,675,400	10,763,600	14,896,343
1928	13,326,263	11,682,450	13,060,851
1929	14,254,446	15,076,600	17,310,484
1930	9,986,742	14,219,937	11,231,417
1931	10,226,986	11,436,182	7,589,116
1932	11,295,305	11,740,708	9,855,991
1933	11,467,850	9,721,995	10,345,094
1934	11,996,327	10,304,270	13,846,634
1935	12,824,910	10,794,484	17,743,657
1936	12,208,210	13,834,170	19,060,826
1937-38†	14,973,115	13,716,990	20,191,495
1938-39	14,842,590	14,089,440	17,999,191
1939-40	18,594,450	12,387,144	16,255,602
1940-41	17,203,200	8,043,180	12,518,688
1941-42	18,774,884	6,862,800	4,235,662
1942-43	19,131,400	2,240,062	
1943-44	21,289,953	2,275,140	10,792,543
1944-45	19,792,288	10,069,807	12,940,215
1945-46	17,677,723	12,796,875‡	4,364,524
1946-47	16,176,838	16,022,480‡	5.876,449
1947-48	15,502,327	15,174,836‡	15,418,581
1948-49	12,554,750	14,152,417‡	15,507,911
1949-50	11,659,181	12,913,393‡	15,313,164

* 1923 figures for 5 months only.

† The New South Wales statistical records were changed from the calendar year to the financial year in 1937.

‡ According to Fairbridge (1948) the post-war trawler catch is almost certainly understated.

from the Government to private enterprise, the quantity of imports increased and continued to increase until 1929 at the expense of the estuarine catch, which was actually lower than the imported quantity of fish from 1926 to 1929 and again from 1933 to 1939, the quantity of imports dropping only during the worst of the depression years in 1930-1932. From 1940 until 1943 the quantity of imported fish dropped, thus increasing the demand for estuarine fish already heightened by the diminution of the trawling fleet. By 1948, the amount of fish imported had once more exceeded the amount taken in the estuaries.

A further reason, which may be classed as social or even political, for the decline in estuarine catch in the years 1946-1950 was the enforcement of the law limiting the issue of licences to persons who derive a substantial amount of their income from personal exertion in the industry. The market thus lost the catch from many men who fished seasonally.

In general the catch per man paralleled that of the total catch. However, the number of men in the fishery was far from constant. Some of the lowest catches and the lowest catches per man were recorded when the greatest number of men were in the industry. This might be regarded as evidence that the catch per man dropped because too many men were fishing, and the total catch dropped because too many fish were taken, so reducing the reproductive or growth potentials. But the period when the number of fishermen increased was over the depression years, when many inexpert fishermen tried to make a living. Many of them were dropping from the industry by 1935 as they were reabsorbed into other industries (see Report of the Fisheries Department of New South Wales for 1935).

The number of fishermen operating was increasing again just prior to the outbreak of the war, but during the whole period 1924-1941 fishing intensity was low, owing both to competition from the trawlers depressing prices or demand and to the fact that the depression years hit the fishing industry in common with other activities.

It is also probably certain that the catches prior to 1940 were understated and thus were higher than recorded, for these figures are records of market handlings plus fish reported as being sold in local districts. As these latter did not pass through a market there is no check on the real amount. Besides the incentive discussed in Section II (*a*) as stimulating fishermen to reveal the true amounts taken during the war years, there was the added incentive to catch more fish as the country was in need of food and the large import fish trade was cut off. In the post-war years competition was revived from both the trawling industry and the import trade, and this, with the increasing cost of materials such as nets, boats, and engines over the last few years, has deterred many fishermen from continuing in the industry.

(iv) *Influence of the Environment on Natural Fluctuations.*—The environment can exert influences upon a fishery by causing fluctuations in stock, due to conditions which may variously cause mortalities or favourable survival rates. The effect of these has been discussed in Section V (*a*) and (*b*). But the indirect effects are important in influencing availability, though perhaps they are not so enduring. The seasons of 1948-49 and 1949-50 were spoilt by heavy flooding (see the Annual Reports of the New South Wales Department for those years). The normal peak catch in April was depressed (Fig. 6). The season 1950-51 was likewise spoilt by floods. There are similar reports, scattered through the Annual Reports of the New South Wales Department, of seasons spoilt by floods. Other effects, not documented in quantitative terms, are doubtless playing a part in altering the suitability of the environment for mullet and other fish. With large-scale land clearing the rate of siltation in the estuaries has increased. The construction of small harbours at the mouths of the larger rivers has involved the building of training walls to control the currents, and these have eliminated the shallows over which mullet and other fish once fed. Drainage schemes have done away with the brackish swamps, adjacent to and opening into the rivers, in which mullet once fed. All these alterations must be affecting the carrying capacity of the rivers for fish; no quantitative data can be presented to bear out this contention, but mention of it is made here to show that these factors should not be left out of consideration in studying the fishery.

(v) *Conclusions on the Status of the Industry.*—It may be seen that such statistics as exist on the estuarine fishery, and thus, by its high correlation, on the mullet fishery, display features that are not inconsistent with any of the possible theories which have been advanced to explain them. However, while the theories of depletion and of long-period natural fluctuations remain unsupported by external evidence, the economic factors of competition and demand were real and are mentioned in the contemporary reports. It would seem illogical to invoke hypotheses on the biological phenomena of the stocks, however valid such hypotheses may have proved in other fisheries, when the economic criteria have been established as facts.

This does not exclude possible operation of biological factors. Fluctuation in number is a characteristic attribute of population (Allee *et al.* 1949). Much of the fluctuation exhibited during the more or less stable periods in the history of the fishery may be due to the existence of such periodicities. But that a long-period fluctuation of considerable amplitude was responsible for the diminished catch over the period 1923-1940 is, in the light of the economic facts, unlikely, nor are there any facts independent of the catch figures to support this idea.

Whether overfishing leading to a depletionary phase might not furnish at least portion of the drop in catch and in catch per man in 1924 is disputable. For the diminution in catch to occur in that year either the spawning stocks must have been reduced alarmingly in the year that the bulk of fish normally maturing in 1924 were spawned, namely autumn

1921, or else an abnormally large number of II+ fish must have been taken in 1923. The catch in 1923 was no larger than that in the preceding nine years, and the catch in 1921 also was no larger than in the preceding seven years. In the absence of age or size frequency data, the possibility that some unusual brood failure in 1921 may have caused the drop in catch cannot be denied with absolute certainty. But the supreme fact which supports the socio-economic interpretation of the catch curves is that this is the only aspect referred to in the contemporary reports. Biological comment is by no means lacking in the Annual Reports of the New South Wales Fisheries Department, and had some unusual failure of the mullet run occurred it would undoubtedly have received mention.

(*d*) *Summary of the Position*

It is concluded that, although the manner in which the catch has fluctuated is not inconsistent with the theories of overfishing and of population cycles, the only explanation of the variations for which there is confirmation which is independent of the catch figures is provided by the economic factor. Competition from both the trawling and the import industries has so lowered the demand through the established channels of trade that a deterrent exists to investment in the estuarine fishery. On the biological side it may be averred that the east coast of Australia is capable of producing from its estuarine fisheries at least 11,000,000 lb. of mullet yearly (Section II), or at least 28,000,000 lb. of all the species at present exploited.

VI. MANAGEMENT MEASURES

Needler (1948) has stated, "To say that fluctuations in abundance are principally caused by factors other than the fishery does not mean that the management of the fishery or control of the fishing effort might not raise the general levels about which the fluctuations might occur."

As stated in Section III, the legal minimum size of mullet permitted to be taken in New South Wales waters was raised in May 1951. In commenting upon this the "Fisheries Newsletter", Vol. 10, No. 4, p. 19, said, "Mr. Roughley (Superintendent of Fisheries, N.S.W.) said the increased legal lengths were necessary owing to the decline of the fish stocks due to too great an intensity of fishing. He said that some years ago the C.S.I.R.O. had discovered that the female mullet did not spawn until it was at least 13 inches and (the) male until it was 12 inches. The C.S.I.R.O. then recommended exactly what the Department was now doing."

In view of the economic facts related above, it seems incorrect to argue that the decline in catch was due to a decline in stocks. Nor is there any evidence that fish are being caught at a predominantly smaller size than in earlier years. Tagging results (Kesteven, unpublished data) reveal a return of tagged fish of only 6.43 per cent. As Kesteven comments, this is undoubtedly lower than the actual proportion retaken, many of which may not reach the investigators. Mortality induced by tagging is believed to be very low on the basis of tests on fish held in ponds. But this is far from being an intense fishing rate. Needler (1948) classified fisheries with a fishing mortality of less than 10 per cent. as being of low intensity. Assuming the returns to be double the actual figure, the mullet fishery would enter the moderately intense classification with fishing mortalities of 10-20 per cent. According to Needler (1948) (and this was not disputed in the discussion that followed this symposium paper), there is great difficulty in making fishing mortality and population estimates from tagging returns in low and moderately intense fisheries, as the degree of accuracy of the method is extremely small.

Kesteven (unpublished data) also purports to give an estimate of total mortality from the longevity of the tags, from which he computes that the average life expectancy of a mullet is 3 years 1 month, "which is in conformity with the observations of earlier work that the majority of fish were caught in their third or fourth year, and this implies a fairly heavy intensity of fishing." In estimating these mortality rates, Kesteven has assumed that the fish are equally available for capture at all seasons and at all ages. It has been shown in Section III (*b*) above that the older age-groups (III+ and older) are only available in quantity during three or four months of the year. It was also shown that the size composition remained much the same during the period 1939-1949 when the number of men fishing (and thus presumably the intensity of fishing) varied from 2751 to 1098. It has been shown too, that in 1903 when far fewer fish were taken and the fishery was expanding, Dannevig (1903) found exactly the same size distribution in the catch. This indicates that it is not the fishing intensity but either natural mortality or, to some extent, lack of availability of the larger fish which makes the representation of the older fish so poor. Natural mortality of the spent fish immediately after spawning is likely to be very high. The spent fish taken in commercial operations are in very poor condition.

The conclusion that the size distribution has persisted in the face of varying intensity of fishing suggests that "uneconomic fishing," in the sense that the fish are caught at too small a size before they have achieved their optimum growth (Higgins 1941), has not caused a drop in catch. As mortality due to fishing is low or at most moderate, there is no indication of an intense fishery. What has been shown is that at least since 1915 the estuarine fishery has suffered from competition with the trawling industry and with the importation of fish products. No management programme will rectify this unless its effect is to provide the public with a more attractive product. It may be argued that the supply of larger mullet may do just this. Let us therefore examine the likely results of the management adjustment of 1951, which was outlined in Section IV (*a*).

The management programme is based on two ideas: firstly, that the fish should be permitted to spawn before being taken, an idea of doubtful validity in the light of the high fecundity of the species; secondly, that a greater weight of fish will be obtained by allowing the fish to grow for a longer period.

A warning should be given that results in one season should not be taken as proof for or against the plan. The present author predicted in a broadcast comment in December 1951 that the 1952 mullet season along the eastern Australian coast would be unusually good. The reasons were these. For three years, 1949, 1950, and 1951, floods disrupted the mullet runs and many of the third-year fish did not mature, presumably because the floods prevented them from obtaining sufficient nourishment to do so. Now, if the contention is correct that a high mortality rate immediately after spawning is responsible for the scarcity of large fish, then a greater number of old fish than usual should be available in 1952, as this factor contributing to mortality will have been much reduced for three successive seasons. It was predicted by the long-range weather forecasting of the Mt. Crohamhurst Observatory that the 1952 season would be a period of low rainfall. It seemed valid, therefore, to expect conditions conducive to a good mullet run with an unusual proportion of large mullet and a forecast was made accordingly. At the time of writing (July 1952), the mullet season is well under way and very good catches are being made. It will be the catch of subsequent seasons which will show whether the regulatory measures are having an effect. As Burkenroad (1951) has pointed out, the only experimental tool the fisheries biologist has is the application of regulatory measures to the fishery. From the scientist's viewpoint, the application of the regulations is principally an experiment from which a large amount of information will be gained. To recommend them, however, the biologist must be convinced that the regulations suggested have the greatest probability of achieving their object. In the present state of biological knowledge there is no guarantee of success. It can only be said that from what knowledge we have this or that measure commends itself as likely to succeed in having the desired effect.

Changing the legal minimum length of mullet from 12 to 13 in. will affect immediately only the fish in that size interval. The result would be only to delay permissible entry of the 12 in. mullet into the fishery by one month during which growth of 1 in. would take place (see Fig. 11). Attainment of 14 in. is deferred by only another month and a quarter. The curve of growth shown in Figure 11 is a mean. The standard deviation about the line is approximately $\frac{3}{8}$ in. (unpublished data). Thus the mean of 13 in. will be achieved by the third week of January by approximately half the 12 in. fish, 68 per cent. will have reached 13 in. by the first week in February and 95 per cent. by the fourth week in February. Third-year fish will commence attaining a size of 14 in. in January, but it will be the end of that month before any number enter the fishery and only half will have attained 14 in. by the end of the growth period in March. In other words, approximately half the third-year fish surviving will be large enough to be fished in their first spawning season. The other half will not be legally catchable until July, when the legal minimum length reverts to 13 in. until the following travelling season. By July the run has ceased in New South Wales. To what extent the fish not captured during the run along the New South Wales coast will enter into the Queensland fishery is unknown, though tagging results (Kesteven 1942, and unpublished data) show that the run is continuous and some fish at least pass from New South Wales to Queensland waters. This class of mullet is poorly represented in the catch from August to December (Section III) in New South Wales, but as far as the data can be trusted the Queensland information shows that fish of this size are still commonly taken in this part of the year. It seems that even with the raised minimum length most of the II+ fish will still be caught in their season of first maturity. Consequently the new regulations are unlikely to increase the number of III+ or older fish.

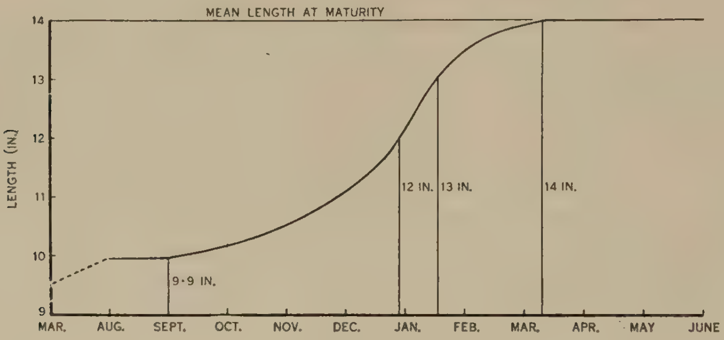

Fig. 11.—Monthly growth curve of third-year mullet (after Thomson 1951).

In growing from 12 to 13 in. each fish gains about 2 oz. in weight (Kesteven 1942, Fig. 4). Then, taking the 1949 figure for the catch shown in Table 1, estimating from Table 10 that 32 per cent. of the catch will be growing the extra 2 oz. per fish, and assuming (1) that no undersized fish are taken, (2) that the fish will all be caught at a length of 14 in., and (3) that no mortality will have occurred, the total gain from the restriction to 13 in. on the 1949 figures would have been approximately 123,000 lb., which is much less than the annual variation in catch (Table 1). It is true that some of the fish would undoubtedly grow larger than 13 in.; it also is certain that some fish would have died in the intervening period, or possibly be removed from the New South Wales fishery by migration.

In growing from 13 to 14 in. mullet would gain approximately another 2 oz. per fish. Taking the monthly catch figures for 1949 published in the Annual Report of the New South Wales Department of Fisheries, and computing the number of fish in this size interval as shown by market measurements for the months March to June, an increase in weight of 207,700 lb. would be effected by raising the length to this size over the months specified. Again the same reservation holds as given above for raising the length to 13 in., but in this case the mortality will be much greater because, as shown above, only about one-half of the fish will have reached 14 in. before spawning and mortality is probably high at this time, or at least availability of large fish is small after the spawning run. The regulations would thus effect a gain of 330,700 lb. odd, which is still small compared with the annual variation, and in any case this is a valid conclusion only if it can be assumed that the stocks are depleted. If the previous conclusion that the mullet stocks are not heavily exploited owing to economic factors is correct, then a similar increase in weight could be effected by taking more II+ mullet, a class of fish which remain in the fishery all through the year. This would be preferable to obtaining the increase in the restricted period when the large mullet are available. This is already a glut season when market handlings cannot cope with the supplies, and the effect of the regulations would be to accentuate this position.

It is thus concluded that the effect of the new regulation adopted in New South Wales will not be as great as expected by its sponsors. In particular, owing to the accumulation of large fish as a result of three wet seasons immediately prior to this year, it will be wise to discount results of the 1952 mullet season. Yet it will be instructive from a biological viewpoint to observe the results of this experiment.

From this review three conclusions on different matters are evident. Firstly, the present systems of statistics in New South Wales and Queensland are incapable of providing estimates of fishing intensity. The factor of time spent in fishing is not available for inclusion in computation. Secondly, it is evident that fisheries biology still lacks a measure of natural mortality rates. This estimation becomes increasingly difficult when older fish are available for capture for only a portion of the year as in the mullet fishery. Finally, it is emphasized that economic factors are of far greater importance in Australian fisheries than has generally been acknowledged.

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THE STABILITY OF THE VITELLINE MEMBRANE AND THE REQUIREMENTS OF DEVELOPING TROUT OVA

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Summary

Rupture of the vitelline membrane by movements of the embryo's tail causes the trout ovum to become permeable to water at about the eyed stage.

Mechanical agitation, direct sunlight, and strong, direct electric light may cause the death of trout ova in the pre-eyed stages by injuring the vitelline membrane. After the pre-eyed stages slight agitation, direct sunlight, and strong electric light do not produce apparent harmful effects on ova. A normal electric lighting system may be used in a hatchery without causing harmful effects.

Dissolved zinc does not cause the death of an ovum by injuring the vitelline membrane.

If the death of a fertile ovum has been brought about without the vitelline membrane being injured the tissues may disintegrate (particularly in the early stages of development) before the ovum turns white. Subsequent treatment with glacial acetic acid will not then show the stage of development reached at death while in some cases the ovum will appear to have been infertile.

The trout ovum contains all substances necessary for development (with the exception of water and oxygen) until the fry begins to feed. Dietary deficiency in trout may result in inferior ova being produced although the parent fish appear to be in excellent condition.

Trout ova will develop normally on flannelette kept damp with distilled water.

I. INTRODUCTION

Under natural conditions the ova of trout are buried in gravel where they are normally protected from mechanical agitation and light until they hatch. Even after hatching it is not until the fry stage is reached that the fish swim actively and are exposed to the sun's rays.

In hatcheries precautions are taken to ensure that ova are not disturbed until they are "well eyed" while light is generally excluded until, as fry, the fish are released into ponds.

The following experiments are mainly concerned with the effects of mechanical agitation and light on ova in relation to hatchery practice.

II. MATERIALS AND METHODS

Ova used in these experiments were obtained from brown and rainbow trout (*Salmo trutta* L. and *S. gairdnerii* Richardson) trapped in the Goulburn River, Victoria, and its tributaries.

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A few extra ova were initially placed in each experimental batch. Twenty-four hours after stripping they were examined to determine whether fertilization had taken place (Affleck 1952*a*).

Ova in glass tanks were examined in situ. Infertile ova in a presumed fertile batch and any excess ova were removed after the examination.

III. RUPTURE OF THE VITELLINE MEMBRANE BY MECHANICAL AGITATION

Gray (1932) showed that the vitelline membrane of a trout ovum is normally impermeable to water and salts. When the membrane is ruptured, however, water enters and salts are lost from the yolk. The loss of salts causes the globulins to be precipitated and the ovum "turns white". Gray also showed that the osmotic stability depends on the age of the ovum, degree of mechanical disturbance, presence or absence of calcium, and type and concentration of exosmotic reagent employed.

TABLE 1

EFFECT OF MECHANICAL AGITATION ON FERTILE AND INFERTILE TROUT OVA

	Turned White			
	Agitated		Control	
Day	Fert.	Infert.	Fert.	Infert.
1	0	0	0	0
2	2	5	0	0
3	4	10	0	0
4	16	28	0	0
5	62	36	0	0
6	80	53	0	0
7	82	54	0	0
8	86	56	0	0
9	90	65	0	0
10	104	71	0	0
11	116	74	0	0
12	122*	100	0	0
13	124	119	0*	0
14	124	136	0	0
15	124	168	0	0
16	124	179	0	0
17	124	188	0	0
18	124	192	0	0
19	124	192	0	1
20	124	193	0	1
21	124	193	0	1
22	124	194	0	1
23	124	194	0	1
24	124	194	0	2
25	124	197	0	2
26	124	200	0	2
40	125†	200	1‡	4

* Embryos eyed. † 75 Hatched. ‡ 199 Hatched.

Krogh and Ussing (1937) and Krogh (1939) showed that ova are permeable to water after the embryo's eyes become visible ("eyed stage") and suggest that at this period the kidneys become functional and expel excess water that enters the embryo. Experiment 1 shows how the permeability of the ovum is restored.

Experiment 1.—Ova from rainbow trout divided into two batches, one fertilized, other not; 200 ova from each batch into separate compartments of a stainless steel wire basket suspended in glass tank; tank filled with water and ova submerged 2 cm.; bubbles of air introduced into water via rubber tube from electric pump. Once a day the basket with ova was removed from tank, shaken gently, and then returned. The two batches, being in the same basket, were thus subjected to the same amount of agitation although the amount on successive days was not necessarily the same. As a control, fertile and infertile ova were placed under similar conditions but not agitated. Results are tabulated in Table 1 and shown graphically in Figure 1.

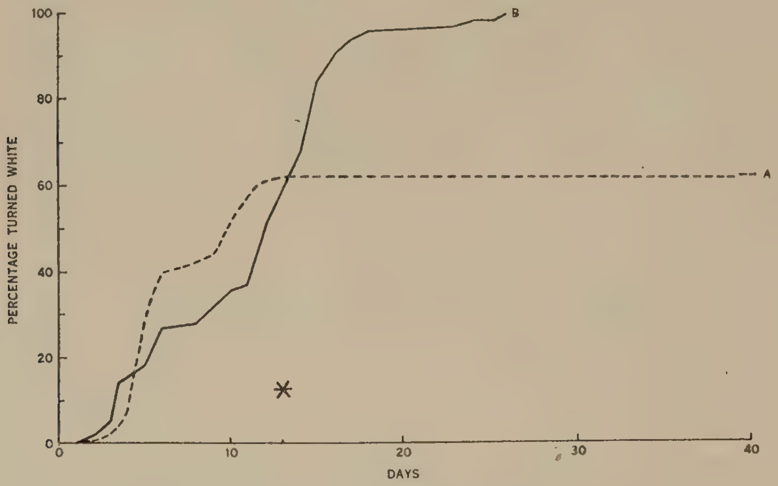

Fig. 1.—Effect of mechanical agitation on fertile (*A*) and infertile (*B*) trout ova. *X*, eyed stage.

The results show:

(1) All ova were not affected to the same degree.

(2) All infertile ova that were agitated eventually turned white, showing that the vitelline membrane had been ruptured and salts lost from the yolk.

(3) In infertile ova that were not disturbed the vitelline membranes retained their impermeable property for a very much longer period than that taken for the embryos to reach the eyed stage.

(4) After the eyed stage agitation did not adversely affect the fertile batch.

(5) The tender period for an individual fertile ovum ends abruptly when the eyed stage is reached.

These results suggest that after the eyed stage in the fertile ovum the vitelline membrane cannot be damaged, or that damage to the membrane does not affect development. However, in the fertile batch of the control, which was not subjected to mechanical agitation, movements of the embryos' tails, which broke the vitelline membranes, were observed at the eyed stage.

It appears therefore that, although the vitelline membrane is not easily damaged by mechanical means when the ovum is shed and when, under natural conditions, it is being buried under gravel, the membrane does become progressively more susceptible to mechanical injury. Under natural conditions the ovum is not normally disturbed and the vitelline membrane remains intact until about the eyed stage when it has become sufficiently susceptible to injury by mechanical means to be ruptured by the first few feeble movements of the embryo's tail. After the vitelline membrane has been ruptured the whole ovum becomes permeable to water.

TABLE 2

EFFECT OF SUNLIGHT ON TROUT OVA

Day	Sunlight (hr.)	Total Sunlight (hr.)	Ova Turned White: In Sunshine (water 4-9°C.) *A*	*B*	*C*	*D*	*E*	Controls (water 4-8°C.) *A*	*B*	*C*	*D*	*E*
1	0	0	0	0	0	0	0	0	0	0	0	0
2	4	4	0	0	0	2	0	0	0	0	0	0
3	4	8	18	28	80	86	0	0	0	0	0	0
4	3	11	28	36	95	100	0	0	0	0	0	0
5	0	11	28	36	96		0	0	0	0	0	0
6	0	11	28	36	96		0	0	0	0	0	0
7	0½	11½	31	37	100		0	0	0	0	0	0
8	0	11½	31	37			0	0	0	0	0	0
9	1½	13	88	92			0	0	1	0	0	0
10	0	13	88	92			0	0	1	0	0	0
11	0	13	89	92			0	0	1	0	0	0
12	0	13	89	92			0	0	1	0	0	0
13	0	13	89	92			0	0	1	0	0	0
14	0	13	89	92			0	0	1	0	0	0
15	1	14	100	97			0	0	1	0	0	0
16	0½	14½		99			0	1	1	0	0	0
17	1	15½		100			0	1	1	0	0	0
18	2	17½					0	1	1	0	0	0
25		41					0*	2	1	0	0	0*

* All hatched.

Wales (1941) noted that ova "leave the tender period gradually". This observation can only apply to a batch of ova where individuals do not reach the eyed stage at about the same time.

IV. EFFECT OF SUNLIGHT ON TROUT OVA

Experiment 2.—Two concrete troughs 60 by 30 by 30 cm., one exposed to sunlight, the other covered as control; water via rubber tube; depth of water 10 cm.; batches of ova from brown trout as follows, *A*, infertile 0 days old; *B*, fertile 0 days (same batch as *A*); *C*, fertile 6 days; *D*, fertile 26 days (almost eyed); *E*, eyed; 100 ova from each batch transferred carefully by means of dip tube to experimental and control troughs. Results are shown in Table 2 and Figure 2.

At the end of the experiment ova in *B* and *D* of the control group were examined and found to have developed normally. Ova in *B* and *D* exposed to sunlight developed normally until they turned white. The results show:

(1) All ova from one batch were not affected to the same degree.

(2) The ova were adversely affected by sunlight only before the eyed stage was reached (not batch *E*).

(3) During the pre-eyed stage the effect of sunlight on infertile ova was similar to that on fertile ova of the same age (*A* and *B*).

(4) The adverse effect of sunlight during the pre-eyed period was greater on older ova ($D > C > B$).

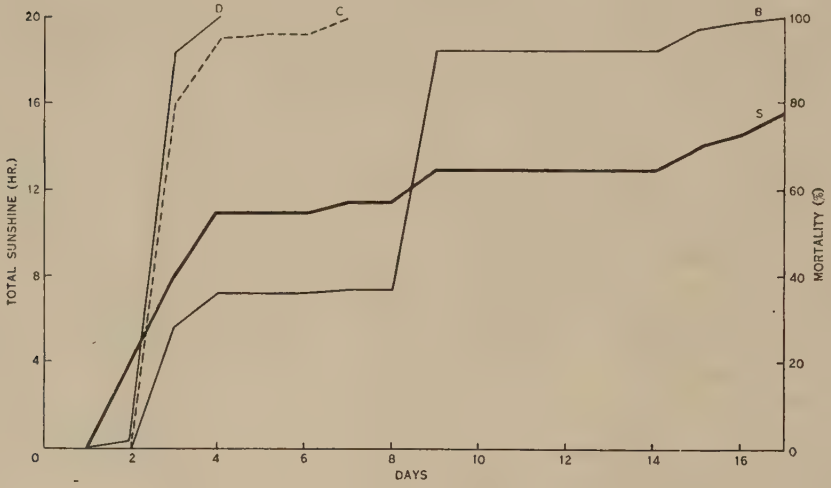

Fig. 2.—Correlation between total sunshine (*S*) and mortality in trout ova. *B*, fertile 0 days; *C*, fertile 6 days; *D*, fertile 26 days.

The effects of sunlight on trout ova are similar to those of mechanical agitation. It appears to disorganize or rupture the vitelline membrane. The effect of sunlight and variation in depth of water is shown in the following experiment.

Experiment 3.—Three concrete troughs, two exposed to sunlight, the other covered as control; water via rubber tube; depth of water 10, 22, and 22 cm. respectively; two batches of ova from brown trout (80 each) to each trough, *X*, fertile 0 days; *Y*, fertile 12 days. Results are shown in Table 3 and Figure 3.

At the end of the experiment ova in the control group were examined and found to have developed normally. In the groups exposed to light ova developed normally until they turned white.

The results show:

(1) The time taken for ova to turn white in the deeper water was longer than that in the shallower water. This difference was emphasized in batch *Y* because of the long period (days 4-16) with little sunlight.

(2) As in the previous experiment, no adverse effect was noted after the eyed stage.

TABLE 3

VARIATION IN THE EFFECT OF SUNLIGHT ON TROUT OVA DUE TO DIFFERENCES IN THE DEPTH OF WATER

Day	Sunlight (hr.)	Total Sunlight (hr.)	Ova Turned White					
			In Sunshine				Control	
			22 Cm. Deep		10 Cm. Deep		22 Cm. Deep	
			X	*Y*	*X*	*Y*	*X*	*Y*
1	0	0	0	0	0	0	0	0
2	4	4	0	0	0	2	0	0
3	4	8	0	0	22	63	0	0
4	3	11	0	5	33	80	0	0
5	0	11	0	5	33		0	0
6	0	11	0	5	33		0	0
7	0½	11½	0	5	62		0	0
8	0	11½	0	5	63		0	0
9	0½	12	10	8	78		0	0
10	0	12	12	8	78		0	0
11	0	12	12	9	78		0	0
12	0	12	12	10	78		0	0
13	0	12	12	10	78		0	0
14	0	12	12	10	78		0	0
15	1	13	21	16	80		0	0
16	0½	13½	30	21			0	0
17	1	14½	37	53*			0	0
18	2	16½	58	53			0	0
19	2	18½	67	53			0	0*
20	4	22½	77	53			0	0
21	5	27½	80	53			0	0
22	5	32½		53			0	0

* Eyed stage.

V. EFFECT OF ELECTRIC LIGHT ON TROUT OVA

Experiment 4.—Three glass tanks—two illuminated by 60-watt, tungsten filament electric lamps (5 and 40 cm. above ova respectively), the third as control not illuminated; ova on stainless steel trays, with four divisions, suspended in tanks; ova from brown trout as follows: *A*, infertile

0 days old; *B*, fertile 0 days (same batch as *A*); *C*, infertile 30 days; *D*, eyed, 30 days (same batch as *C*); 24 ova from each batch in each tray; ova 1.5 cm. below surface. The effects of illumination are shown in Table 4.

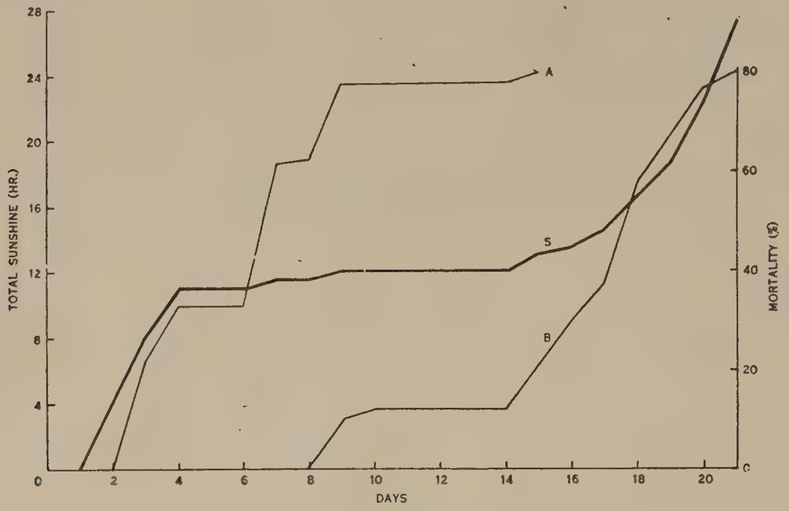

Fig. 3.—Variation in the effect of sunlight (*S*) on trout ova due to differences in depth of water. *A*, 10 cm. deep; *B*, 22 cm. deep.

Ova in *B* exposed to lamp 5 cm. above developed normally until they turned white.

The results show:

(1) All ova in one batch were not affected to the same degree.

(2) With lamp 40 cm. above ova (the minimum distance likely to be encountered in a hatching house) no adverse effects were noted.

(3) With lamp 5 cm. above, pre-eyed ova were adversely affected.

(4) With the lamp 5 cm. above, the effect on infertile ova was similar to that on fertile ova of the same age during the pre-eyed stage.

(5) The adverse effect was greater on old infertile ova than that on new infertile ones.

(6) A hatching house may be illuminated by electricity if the lamps are not too close to the ova.

Deterioration of the vitelline membrane due to age was undoubtedly responsible for the few infertile ova eventually turning white in the control batch and in that with the lamp 40 cm. above.

These results suggest that the action of electric light on trout ova is similar to that of sunlight.

VI. IMPERFECT OVA

On being stripped some trout ova have a very translucent appearance. Hatchery personnel often refer to them as "glassies". Examination of 38 trout showed that these ova occur amongst normal ones in the body cavity and also amongst unshed ova in the ovary.

Some "glassies" were stripped into a Ringer solution and retained their very translucent appearance. Others stripped into water turned white almost immediately, showing that the vitelline membranes were incomplete.

TABLE 4

EFFECT OF ELECTRIC LIGHT ON TROUT OVA

Day	Ova Turned White											
	Lamp 5 Cm. Above				Lamp 40 Cm. Above				Control			
	A	*B*	*C*	*D*	*A*	*B*	*C*	*D*	*A*	*B*	*C*	*D*
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	2	0	0	0	0	0	0	0	1	0
3	0	0	2	0	0	0	0	0	0	0	1	0
4	0	0	16	0	0	0	0	0	0	0	1	0
5	0	0	24	0	0	0	0	0	0	0	3	0
6	0	0		0	0	0	0	0	0	0	3	0
7	0	0		0	0	0	0	0	0	0	3	0
8	0	0		0	0	0	1	0	0	0	3	0
9	12	14		0	0	0	1	0	0	0	3	0
10	21	22		0	0	0	1	0	0	0	3	0
11	24	23		0	0	0	1	0	0	0	3	0
12		23		0	0	0	1	0	0	0	3	0
13		24		0	0	0	1	0	0	0	3	0
14				0	0	0	2	0	0	0	3	0
15				0	0	0	2	0	0	0	3	0
30				0*	0	0	3	0*	0	0	5	0*
60					5	0*	10		2	0*	7	

* All hatched.

Infertile and fertile ova at an early stage of development were placed in a Ringer solution and agitated until the vitelline membranes were ruptured. All the ova became very translucent.

It appears therefore that the very translucent appearance of some trout ova before they are placed in water is due to an incomplete or ruptured vitelline membrane. Until placed in water salts do not escape from the yolk and globulins are not precipitated because the ova are surrounded by body fluids containing salts.

VII. Effect of Zinc on the Vitelline Membrane

Dissolved zinc is toxic to trout ova even in very small concentrations (Affleck 1952*b*) although the effect on individual ova varies considerably. In experiment 6 the effects of zinc on fertile and infertile ova are compared.

Experiment 6.—Two glass tanks; in one galvanized iron tray with two compartments, the other, as control, with stainless steel tray; water via galvanized iron pipe to experimental tank and via rubber tube to control; ova from rainbow trout as follows: *A*, infertile 0 days old; *B*, fertile 0 days (same batch as *A*); 25 ova from each batch in each basket. The effects of the zinc are shown in Table 5.

Table 5

EFFECTS OF ZINC ON FERTILE AND INFERTILE TROUT OVA

Day	Ova Turned White			
	Galvanized Tray		Control Tray	
	A	*B*	*A*	*B*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	2	0	0
5	0	3	0	0
6	0	10	0	0
7	1	14	0	0
8	1	20	0	0
9	1	23	0	0
10	1	24	0	0
11	1	24	0	0
12	1	25	0	0
30	1	25	0	0*

* All eyed.

The results show that only fertile ova were affected by zinc during the pre-eyed stage. If the vitelline membrane had been adversely affected the infertile ova would have turned white. At the conclusion of the experiment the trays were shaken and as a result the infertile ova turned white.

It may be concluded, therefore, that dissolved zinc does not kill trout ova as a result of disorganizing the vitelline membrane.

VIII. Dead Ova and the Glacial Acetic Acid Technique

If dead ova are placed in glacial acetic acid they are cleared and the embryos turn white (Rutter 1902).

In a hatchery, ova are not assumed to be dead during the pre-eyed stages until they turn white. When ova turn white, embryos cannot normally be seen until the ova have been cleared.

By keeping ova in glass tanks, illuminated from below by electric lamps, it is possible to observe if fertilization has taken place and then watch the developments *in situ*. It has been noted that ova do not always turn white when development stops and that embryonic tissues may disintegrate, particularly during the early stages of development, before the ova eventually turn white. This could be explained if death was brought about by causes other than the rupturing of the vitelline membrane. Subsequent treatment with acetic acid will not then show the stage at death while in some cases all tissues may have disintegrated and the ova, after treatment, may appear to have been infertile.

IX. SOME DIFFERENCES IN TROUT OVA

It is noticeable that ova from most hatchery-reared trout, or from fish that have been kept at a hatchery for a period of a year or more, are very pale in colour when compared with those obtained from wild fish. The following representative experiments show the comparative mortality experienced amongst batches of ova from wild rainbow trout trapped just prior to stripping and from wild fish retained at the hatchery and fed on raw bullocks' liver for 1-2 years.

TABLE 6

COMPARATIVE MORTALITY AMONGST ALEVINS AND OVA OBTAINED FROM WILD FISH AND FROM FISH RETAINED AT THE HATCHERY FOR 1-2 YEARS

	Ova Stage			Alevin Stage		
Ova From	Total Fertile Ova	Hatched	Hatch (%)	Initial Number	Survivors	Survival (%)
Wild fish	200	200	100	20	19	95
Hatchery 1 yr.	200	173	87	20	13	65
Wild fish	200	198	99	20	20	100
Hatchery 2 yr.	200	28	14	20	0	0

Experiment 7.—Two glass tanks; stainless-steel wire baskets with two compartments; tanks filled with distilled water; bubbles of air introduced into water via rubber tube from electric pump. First tank—200 ova from wild fish (control) placed in one compartment, 200 ova from fish fed on raw liver for 1 year in the other. Second tanks—200 ova from wild fish (control), 200 ova from fish fed on raw liver for 2 years. After hatching 20 alevins only retained from each group so as to avoid effects due to overcrowding. Alevins kept for 3 weeks when, although most of yolk absorbed, specimens of each group could still be recognized by colour of yolk. Results are shown in Table 6.

These results show that:

(1) Mortality amongst ova and alevins from fish feeding on natural food was low.

(2) Mortality amongst ova from fish feeding on raw bullocks' liver for 1 year was low whilst for the alevin stage it was comparatively low.

(3) Mortality amongst ova from fish feeding on raw bullocks' liver for 2 years was very high while for the alevin stage it was 100 per cent.

Fish retained at the hatchery (60) were kept in a pond having gravel sides and bottom and an area of approximately half an acre. A small flow of water from Snobs Creek (for analysis see Affleck 1952*b*) passed through the pond, which contained little aquatic vegetation or natural fish food. The fish were fed twice a day on raw bullocks' liver which formed the bulk of their food although some terrestrial insects, etc. were also eaten.

All fish used were 4 years old and scale readings showed that the growth rate of fish in the hatchery (which appeared to be in excellent condition) feeding on liver was approximately twice that of the wild fish for the same periods.

Ova from the wild fish were a brilliant red-orange; from fish retained for 1 year they were pale yellow; while from fish retained for 2 years the ova were a pale green-yellow.

Trout ova and alevins developing in aerated distilled water can absorb little or no substances from the water. Ova must, therefore, contain all the materials necessary for development, with the exception of water and oxygen, until the fry begin to feed. It is reasonable to suppose that the differences observed between the groups of ova were due, at least partially and probably almost entirely, to differences in the diet of the parent fish.

The adverse effects of dietary deficiency on the ova produced must be more severe in trout (where a relatively long time elapses from fertilization of the ovum to the period when the fry begin to feed) than in species of fish where fry begin feeding at, or soon after, hatching.

X. THE REQUIREMENTS OF DEVELOPING TROUT OVA

The following experiment shows the probable minimum requirements necessary for the development of trout ova.

Experiment 8.—Shallow enamelled tray approx. 33 by 25 by 2 cm. in which a small drainage hole had been made in one corner of the bottom; enamelled dish approx. 12 by 7 by 3 cm. placed at end of tray as reservoir; piece of flannelette (previously washed) on bottom of tray with a projection (acting as wick) into reservoir; ova placed on flannelette and covered with washed cotton mosquito netting (Plate 1); the whole covered by inverted enamelled tray. Ova were left undisturbed until eyed, when infertile ones were removed. Just prior to hatching (indicated by colour of yolk appearing more brilliant owing to chorion becoming thinner) the ova were transferred to stainless steel trays. Some results obtained with ova from wild brown trout are shown in Table 7.

TABLE 7

MORTALITY AMONGST BROWN TROUT OVA DEVELOPING ON A DAMP CLOTH

Total Ova (Fertile and infertile)	Eyed	Eyed (%)	Hatched	Hatched (%)
847	824	97	821	97
683	671	98	671	98
813	799	98	795	98
751	701	93	694	92

The results show:

(1) The volume of water per ovum required for development is small.

(2) Only a very small flow of water over the ovum is really necessary.

Under natural conditions, where ova are buried under gravel, the flow of water over them is extremely small. In some hatcheries, however, mortality is high unless the flow of water through the hatching troughs is comparatively large. In such cases it is suggested that water is polluted on its way through the hatchery, possibly by flowing through metal pipes, and that an increase in flow merely decreases the concentration of the toxic substances.

XI. CONCLUSIONS

(1) There are great differences, in many respects, between individual trout ova.

(2) The tender period of an ovum ends abruptly when the vitelline membrane is ruptured by movements of the embryo's tail at about the eyed stage and the ovum becomes permeable to water.

(3) During the pre-eyed stages direct sunlight and strong, direct electric light may cause the death of a trout ovum by injuring the vitelline membrane.

(4) Eyed ova are not adversely affected by sunlight or electric light.

(5) A hatching house may be illuminated by electricity.

(6) Dissolved zinc does not stop the development of a trout ovum by damaging the vitelline membrane.

(7) The volume and flow of water per ovum need only be very small.

(8) "Good trout ova" contain all substances necessary for development, with the exception of water and oxygen, until the fry begin to feed.

(9) The quality of ova is largely determined by diet of the parent fish.

(10) Dietary deficiency in trout may result in inferior ova being produced although the parent fish may appear to be in excellent condition.

(11) Once "good ova" are fertilized few losses should be experienced up to the time the fry begin to feed.

(12) Because few or no substances are removed from water, provided that it is well oxygenated, only two kinds of water exist for the developing trout ovum, viz. water and polluted water.

(13) Trout ova will develop normally on flannelette kept damp with distilled water.

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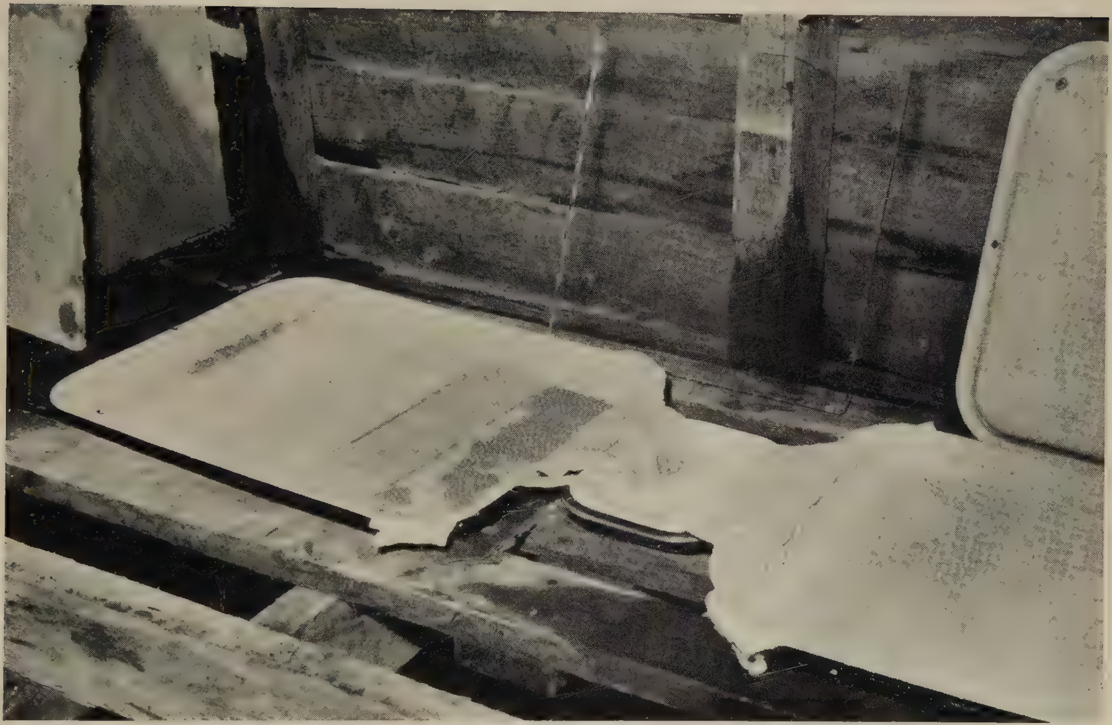
VITELLINE MEMBRANE AND DEVELOPING TROUT OVA



Batches of trout ova developing normally on flannelette kept damp with distilled water. The cover of mosquito netting has been removed from one batch.

TAGGING OF SCHOOL SHARK, *GALEORHINUS AUSTRALIS* (MACLEAY) (CARCHARHANIDAE) IN SOUTH-EASTERN AUSTRALIAN WATERS

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Summary

In south-eastern Australian waters, 5835 school sharks have been tagged since 1947. The two techniques used and the effects of some of the tags on the fins and body walls are described.

It was found that the percentage return from experiments using both internal and fin tags was three times that from experiments using only fin tags. No significant difference was found in the numbers of white and grey Petersen disc fin tags returned. No deterioration has been detected in these tags and the silver tagging wires have not shown any appreciable signs of wear.

Under natural conditions the incision made in the body wall for this insertion of the internal tag has been found to have healed completely within 2 months. Often there is no sign of the scar after 12 months.

I. INTRODUCTION

Only during the last decade has any particular attention been given to tagging elasmobranchs. In 1936, Steven reported that 700 skates and rays had been tagged and released around the British Isles, and according to Rounsefell and Kask (1943) only 1005 had been tagged in all European waters up to 1940. Since then over 6000 sharks of three different species have been tagged in American waters. Foerster (1942) reported the release of 564 Pacific dogfish (*Squalus suckleyi* (Girard)) off British Columbia up to 1942 and Templeman (1944) in the same year off Newfoundland released 279 *Squalus acanthias* (Linnaeus). Another 4404 Pacific dogfish were tagged and released in the waters of the State of Washington by Bonham *et al.* (1949). In Oregon waters, Westrheim (1950) released 427 soupfin sharks (*Galeorhinus zyopterus* (Jordan and Gilbert)), and another 118 have been tagged in Californian waters (Herald and Ripley 1951).

Even though Rounsefell and Kask (1943) commented on the lack of organized knowledge of tagging methods as far back as 1940, there is still an absence of details about tagging elasmobranchs. For that reason it was considered desirable to make known these observations on different tagging techniques used over the past 6 years on almost 6000 school sharks (*Galeorhinus australis* Macleay) in the waters of south-eastern Australia.

In 1942, G. P. Whitley used internal tags for 22 school sharks released in Tasmanian waters, but it was not until 1947 that a comprehensive tagging programme was undertaken, as a part of the general investigations on the biology of this species. The two methods of tagging tried were the

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external Petersen disc tag attached to the first dorsal fin and the Nesbit internal body cavity tag. The Petersen disc method was adopted after a series of preliminary tests with external tags in the experimental pool of the C.S.I.R.O. Marine Biological Laboratory, Cronulla, N.S.W. Three years later the internal tagging technique was introduced in an attempt to check the suspected loss of fin tags. This method was not adopted at the beginning of the investigations because as there was no external mark, fishermen do not recover the tag until the carcase is being cleaned and by that time the head has usually been cut off and total length measurements cannot be taken.

II. Equipment and Methods

(*a*) *External Tagging*

At first, a white plastic numbered Petersen disc tag (16 mm. diameter and 1 mm. thick) was fastened to one side of the first dorsal fin by a silver wire passing through the fin to a white plastic disc of the same dimensions on the other side. Later this plain white disc was replaced with a clear celluloid (cellulose nitrate) disc. In April 1950, the use of white numbered tags was discontinued and grey-coloured numbered discs of similar specifications used. Both were made by the same English manufacturer. The change was made because, as many returned white tags had deep scratches, it was thought that the contrast in colours between the white tag and the fin might have caused other fish to snap at the tags.

For the purpose of piercing the thickened base of the first dorsal fin of school sharks, a simple awl was found most satisfactory. The metal part was 3 mm. in diameter except for the 1 cm. tip which was ground down to 1 mm. diameter (Plate 1).

The pliers used for cutting and bending the wire were electrician's long-pointed pliers not modified in any way.

The non-corrosive wire used throughout this investigation was made from pure silver, hot drawn, 0.84 mm. diameter (21 S.W.G.), and proved most satisfactory. It showed none of the disadvantages experienced by Calhoun, Fry, and Hughes (1951). These workers found that friction from the tags reduced the diameter of silver wire. Even after 2 years in the open sea the wires showed no such wear and likewise no deterioration was found in the discs. All the knotted wires used were prepared in the laboratory workshop and had a 5 mm. closed loop in the form of a simple knot at one end of a straight 3 cm. length (Plate 1).

The method of attaching the tags was as follows: the free end of the wire, on which was threaded the numbered tag, was passed through the hole pierced by the awl in the dorsal fin. On the other side of the fin a blank tag was put on the wire and all wire in excess of about 1.5 cm. was cut off. By taking this cut end firmly in the tips of the pliers so as to leave about 3 mm. projecting, the pliers were turned through 270° to form a closed loop 5-8 mm. in diameter with 3 mm. of the free end projecting at right angles to the stem of the wire. Without removing the pliers, the plane of the closed ring was bent at right angles over the extension of the free end, bringing the latter under the bend and the plane of the loop parallel to that of the disc tag (Plates 1, 3). In this position the loop served as an effective stop for the blank tag, and sharp bends in the wire were reduced to a minimum. Allowance was always made for some movement of both tags. If the tags were fastened too tightly against the skin they tended to erode it, causing sores from which the tags were easily torn.

(*b*) *Internal Tagging*

It was found that scalpels with sharp detachable blades were best for making the necessary incision in the body wall. This was made on the left flank parallel to the muscles in the lower half of the body immediately below the posterior half of the first dorsal fin (Plate 2). Here, the body wall is thinnest and there is less likelihood of damaging the internal organs. Anterior to this position the liver is likely to be incised whereas posteriorly the spiral valve may be punctured. The peritoneum of the body cavity of school sharks is surprisingly tough and unless a sharp scalpel is used undue pressure has to be exercised to penetrate it. Under such circumstances damage to internal organs may result from the sudden breaking of the lining. In Plate 2 is shown the method of inserting the internal tag in school sharks.

Two sizes of white plastic internal tags have been used. The smaller tags measure 35 mm. in length by 10 mm. at their wider end and the larger 40 by 23 mm. The smaller tag was used on sharks up to 75 cm. in length, the larger tag on those above this size range. The instructions and numbers printed on these tags were unaffected after 3 years in the body cavity of the sharks.

Small sharks were measured on a 1-m. measuring board but for the large, heavy adults a special measuring trough was designed (Fig. 1). This trough is open at the bottom to allow the right pectoral fin to project through, thereby assisting with the holding of these strong sharks. Metre rules recessed into the wood in convenient positions permit all necessary measurements to be read off. Recessing of the rules is essential, otherwise the rough skin soon obliterates the calibrations.

III. RESULTS

Altogether 5835 school sharks have been tagged, the majority of which were juveniles caught by handlines or nets in inshore waters of bays and estuaries. Initially all tagging was done from shore-based centres, but from 1948 the larger sharks in offshore waters were caught by longlining from the research vessel. The tag releases have been separated into those of inshore (bay, inlet, and estuary) origin (4695) and those released offshore (1140).

During these operations three methods involving two different techniques were tried:

(1) Petersen disc tags attached to the first dorsal fin.
(2) Body cavity tags.
(3) Double tagging (combination of 1 and 2).

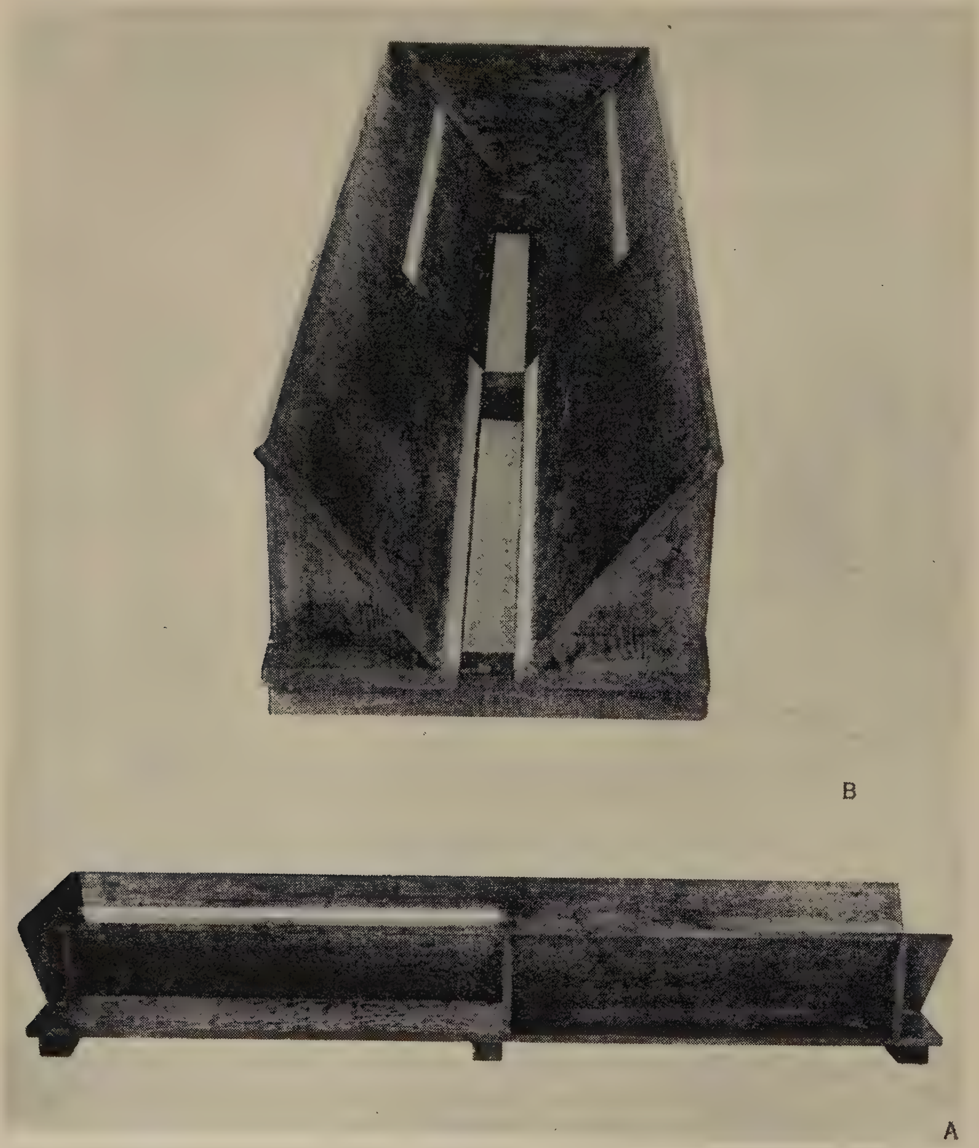

Fig. 1.—Measuring trough for large sharks. *A*. Side view to show deck clearance and section for holding tagging gear. *B*. The 2-m. trough for measuring large school sharks. Note the open bottom for holding the pectoral fin and permitting drainage.

The number tagged by each method in the two different operations over the period 1947-1952 is given in Table 1.

It will be seen that very few sharks (1.8 per cent. of the total number) have been released with the internal tags alone. Initially, it was contemplated that a large number of sharks could be marked this way but because of the benefits expected to accrue from combining both this and the Petersen disc method, it was decided to double-tag all sharks. Even if sharks lost their fin tags they could be identified by the presence of the internal tag in the body cavity. By this means it would also be possible to assess the rate of loss of dorsal fin tags. An occasional shark was caught with a split dorsal fin, suggesting the loss of its fin tag. Also fishermen catching fin-tagged sharks tended to remove the tags and release the undersized sharks, the subsequent movements of which were lost through the lack of a second identifying tag.

TABLE 1

NUMBER OF SHARKS TAGGED BY DIFFERENT METHODS

Method		1947	1948	1949	1950	1951	1952	Total	Percentage of Total Releases
1. Dorsal fin tags	Inshore	621	673	909	959	47	—	3209	
	Offshore	—	89	280	2	—	—	371	
	Total	621	762	1189	961	47	—	3580	61.35
2. Internal tags	Inshore	—	—	1	—	1	1	3	
	Offshore	—	—	102	—	—	—	102	
	Total	—	—	103	—	1	1	105	1.80
3. Double tagging	Inshore	—	—	8	503	839	133	1483	
	Offshore	—	—	129	338	200	—	667	
	Total	—	—	137	841	1039	133	2150	36.84
Grand total		621	762	1429	1802	1087	134	5835	

TABLE 2

NUMBER OF RETURNS FROM DIFFERENT TAGGING METHODS

Method	Inshore		Offshore		Total No.	No. of Sharks Tagged	Percentage Return
	Returns	No. Tagged	Returns	No. Tagged			
1. Fin tags only	71	3209	4	371	75	3580	2.09
2. Internal tags only	1	3	2	102	3	105	2.85
3. Double tags					125		5.81
Fin tag present	56	1483	5	667	61	2150	2.84
Fin tag lost	53		11		64		2.97
	181	4695	22	1140	203	5835	3.48

Since the practice of double-tagging was instituted many sharks have been caught twice. The benefit derived from double-tagging can be seen by the increase in the percentage returns, which have already risen to nearly 6 per cent. As time goes on it is expected that the number of returns will gradually increase. The returns for each of the different tagging methods from both estuarine and research vessel teams are given in Table 2.

By double-tagging sharks the percentage return is about three times greater than that by fin tagging only (2.09 per cent).

Because of the low number of releases with internal tags alone no valid comparison could be made between methods 2 and 3, but this was not so between fin tags in methods 1 and 3. These external tags show very similar percentage returns. As white tags were used almost exclusively prior to double-tagging a comparison of the results obtained with tags of each colour was desirable.

The number of sharks tagged with white Petersen discs was 3259 and with grey 2471. The returns from these have been summarized in Table 3.

TABLE 3

COMPARISON OF RETURNS OF COLOURED FIN TAGS

Tag Colour	1947	1948	1949	1950	1951	1952	Total	Percentage Return
White								
Returns	32	11	22	—	—	—	65	1.99
Releases	621	762	1326	550	—	—	3259	
Grey								
Returns	—	—	—	39	32	—	71	2.87
Releases	—	—	—	1252	1086	133	2471	
Total releases	621	762	1326	1802	1086	133	5730	2.37

From Table 3 it would seem that grey tags were slightly better than white tags, but this is not the case. The figure for grey tags has been given a bias by the large number of grey tags obtained from George Bay, Tasmania, where more sharks were released with grey tags (284) than with white tags (35). Consequently the addition of 26 grey tag returns and only 4 white returns from this bay to the results for each colour from other areas gave a total figure from which a wrong conclusion may be drawn. The fin tag returns from this bay averaged 10 per cent., twice as high as that from any other single area.

However, if the percentage returns for each colour from each area were compared there was no significant difference between the two results. In George Bay, the percentage return for white tags was 11.4 and grey 9.1 per cent., and this close correlation was obtained even when such a low number of white tags was used. No difference between colours was obtained in Port Phillip Bay, where the returns from sharks with white tags (618) were compared with 456 with grey tags. In this case the fin tag returns were only half as good as the former area yet there was a good correlation between results for the two colours (5.17 per cent. for white and 4.16 per cent. for grey). As the lengths of the juvenile population in Port Phillip Bay vary from year to year, the 1947 results for white tags were compared with the 1951 grey tag results, for in these years the sizes were almost identical. In each case white tags have been in use longer than grey and a slightly higher percentage return is not unexpected.

Even when returns for each particular tag colour were compared against size of sharks and duration of freedom, there was still no definite evidence that one colour was responsible for better percentage returns than the other (Table 4).

Four-fifths of the total returns were reported within 4 months of release. These returns after such a short period were due solely to the intensity of fishing in Port Phillip Bay and George Bay, where immature sharks were accidentally caught. However, provided the bias in the results from George Bay is recognized, it can be seen that there is no significant difference between the results obtained with white and grey tags. This may not always be the case with those smaller species of elasmobranch fishes or teleostean species which may be subjected to greater predation than school sharks. No specific predator is known for school sharks although they are attacked, when caught on the long line, by the seven-gilled shark, *Notorhynchus cepedianus* (Peron).

IV. THE EFFECT OF TAGS ON THE TISSUES

(*a*) *Petersen Disc Tag*

It has been found that, since the cartilaginous rays of the dorsal fins of young sharks are softer than those of the older sharks, there is a greater loss of fin tags from the juveniles less than 1 year old. Moreover, the loss of fin tags among older juveniles is also high in areas where zostera-like plants flourish. As the sharks search for their food among these plants, strands catch on tags and wires, causing the fin to tear. Once the fin is slightly torn the constant friction from the wire causes a pronounced irritation of the raw edges of the split, and it is not long before the tag wires tear out completely. In areas carrying less vegetation such fin damage is rare.

Torn fins are frequently observed where mesh nets are commonly used and tags are often found lodged in the nets, having been torn out in the sharks' struggles to escape. Sharks which have lost their tags through being entangled in weeds or nets are easily recognized and some examples of damage to fins by wires and tags are shown in Plate 3. In Plate 3, Figure 1, the tag has been correctly applied, leaving some free movement of the two tags and, as a consequence, there is no damage or tearing. The fin is viewed through the transparent backing disc. The second example (Plate 3, Fig. 2) shows an incompletely torn fin with damage to the edges of the split and some erosion to the skin caused by friction from the tag. The area immediately surrounding the base of the tear is darkened and shows the initial response of the irritated tissue.

Plate 3, Figure 3, demonstrates further stages of damage resulting from continued friction of the tag wire whereas Figure 4 shows a clean tear with subsequent rapid healing. These illustrations are all from juvenile sharks 525-675 mm. in length caught within the estuaries of Port

TABLE 4

COMPARISON OF WHITE AND GREY TAG RETURNS IN RELATION TO SIZE AND DURATION OF FREEDOM

Length When Tagged (mm.)	Duration of Freedom (weeks)										Total
	0-1	1.1-2	2.1-4	4.1-8	8.1-16	16.1-32	32.1-64	64.1-128	128.1-256		
301-400	1/1		3/1	1/0			0/1			5/3	8
401-500		0/2	1/2	5/2	2/3	0/3		1/0		9/12	21
501-600	2/0	1/0	4/2	15/3	8/11	3/5	0/2		1/0	34/23	57
601-700		0/1	1/4	1/7	4/7	0/4	0/1	0/1		6/25	31
701-800			1/0	0/1	2/1	0/1				3/3	6
801-900				1/1				1/0		2/1	3
1001-1100								1/0		1/0	1
1401-1500				1/0	1/0	1/1	0/1			3/2	5
1501-1600							0/1	1/0		1/1	2
	3/1	1/3	10/9	24/14	17/22	4/14	0/6	4/1	1/0	64/70	
Total	4	4	19	38	39	18	6	5	1	134	134

Numerator = white tag returns. Denominator = grey tag returns. Two returns omitted owing to lack of certain information about recovery.

Phillip and George Bay. The sharks had been free for 6, 4, 8, and 13 weeks respectively and Nos. 2, 3, and 4 were returned from George Bay.

Whereas tagging wires are the main cause of split fins, tags have produced erosion of the fin of a school shark (742 mm.) recaptured in Port Phillip Bay after only 75 days' freedom. In this case both sides of the fin had been eroded down to the cartilaginous skeletal rays and erosion was the result of attaching the tags too tightly. It has been found that tags with free movement cause little or no erosion to the fins. The tip of the free end of the silver wire rubbing the skin had caused the removal of some of the denticles from the skin of the first dorsal fin (Plate 3, Fig. 5). During the tagging operation the excess wire had not been removed and the tip of the wire beneath the bend had projected beyond the end of the tag and caused this minor injury. This particular shark was longlined in 180 fathoms, hauled to the surface, tagged, and released again in the same locality and was free for 2 years and 4 months before being recaptured 140 miles distant in 80 fathoms. During this time the total effect of the tag wire on the skin was small.

It is desirable that the rough edges of all tags should be smoothed with very fine glass or emery paper. Rounsefell and Kask (1943) emphasized the need for the removal of rough edges from all kinds of tags.

(*b*) *Nesbit-Internal Tags*

The question most frequently asked about this method is the time taken for the incision wound to heal. Under natural conditions, the walls of the incision knit together and heal from the inside outwards. Within 30 days of tagging the greater portion of the wound has healed and only the external layer of skin has to close completely (Plate 4, Fig. 1). Nine weeks after tagging, the wound had healed completely exteriorly (Plate 5, Fig. 2) and the only visible sign on the interior wall is a slight pucker in a depression (Plate 4, Fig. 3). Within 12 months, it is often impossible to detect a scar on either side of the body wall. This observation applies to school sharks of all sizes.

In most cases the internal tag is found lying on, or under, a lobe of the liver on the ventral side of the body cavity. In Plate 5 are shown the positions of two tags immediately after the sharks had been opened. In Plate 5, Figure 2, the tip of the liver had been folded back to show the tag. Though the majority of tags are located in the anterior region of the body cavity some have been found lying alongside the spiral valve. In no instance has any injury or damage to the internal organs been observed.

V. ACKNOWLEDGMENTS

The author wishes to acknowledge the assistance with tagging he has received from the members of the Division's Tasmanian field station and the master and crew of the research vessel *Derwent Hunter*.

Photographs used in Plates 1, 3, and 4 were prepared by Mr. H. J. Read; those in Figure 1 by the Division's technical staff under the supervision of Mr. A. Proctor. Photographs in Plate 2 were obtained with the cooperation of the Visual Aids Centre of the Tasmanian Education Department.

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EXPLANATION OF PLATES 1-5

PLATE 1

Tags and equipment used for tagging school sharks.

PLATE 2

Method of inserting internal tags.

Fig. 1.—The incision in the left flank below the first dorsal fin.

Fig. 2.—The narrow end of the internal tag inserted into the body cavity of a juvenile school shark.

PLATE 3

External fin tag damage.

Fig. 1.—Tag correctly applied. No damage (43 days after release).

Fig. 2.—Partially torn fin with tissue erosion (30 days after release).

Fig. 3.—Completely torn dorsal fin (57 days after release).

Fig. 4.—Partially healed tear (13 weeks after release).

Fig. 5.—Erosion from lack of free movement (75 days after release).

Fig. 6.—Skin abraded by tagging wire (120 weeks after release).

PLATE 4

Healing of internal tag incision.

Fig. 1.—Incomplete external healing of incision after 30 days.

Fig. 2.—Complete external healing after 66 days (tag 396).

Fig. 3.—Scar tissue formed on internal body wall (tag 396).

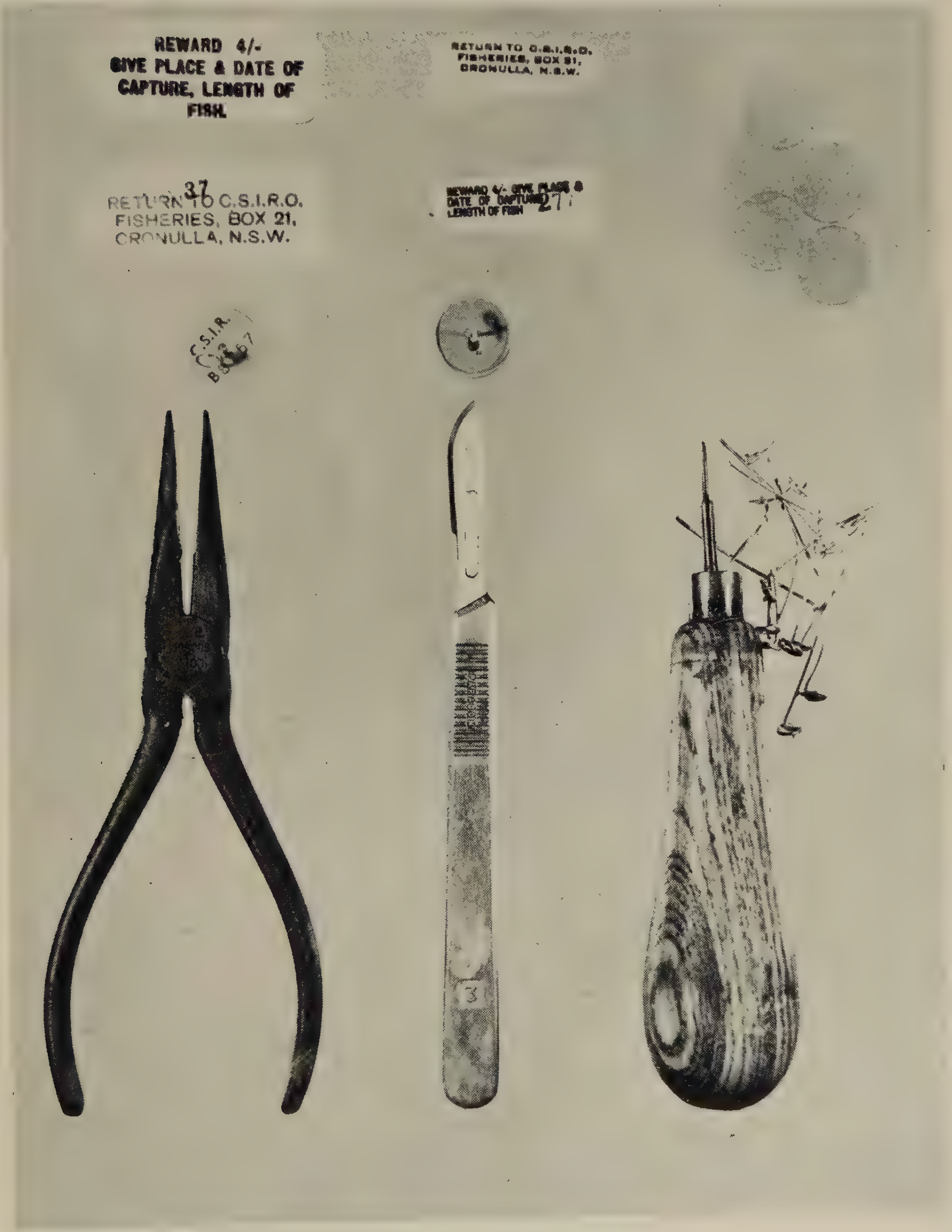
PLATE 5

Internal tags in situ.

Fig. 1.—Internal tag lying on ventral surface of liver (111 days after release).

Fig. 2.—Lobe of liver folded back to show position of tag on ventral surface of stomach (122 days after release).

TAGGING OF SCHOOL SHARK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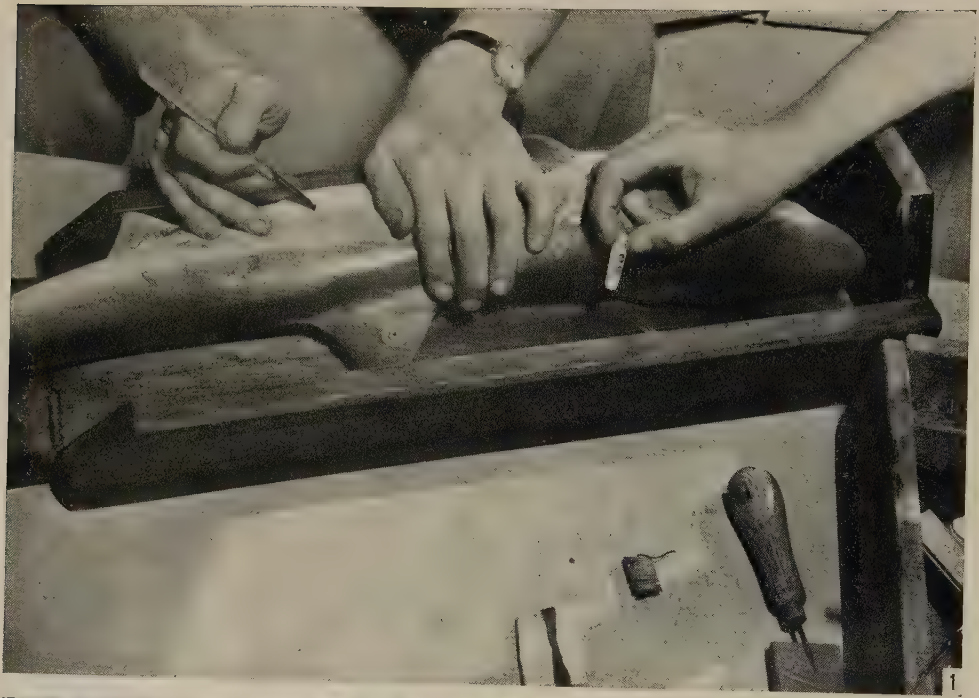
TAGGING OF SCHOOL SHARK



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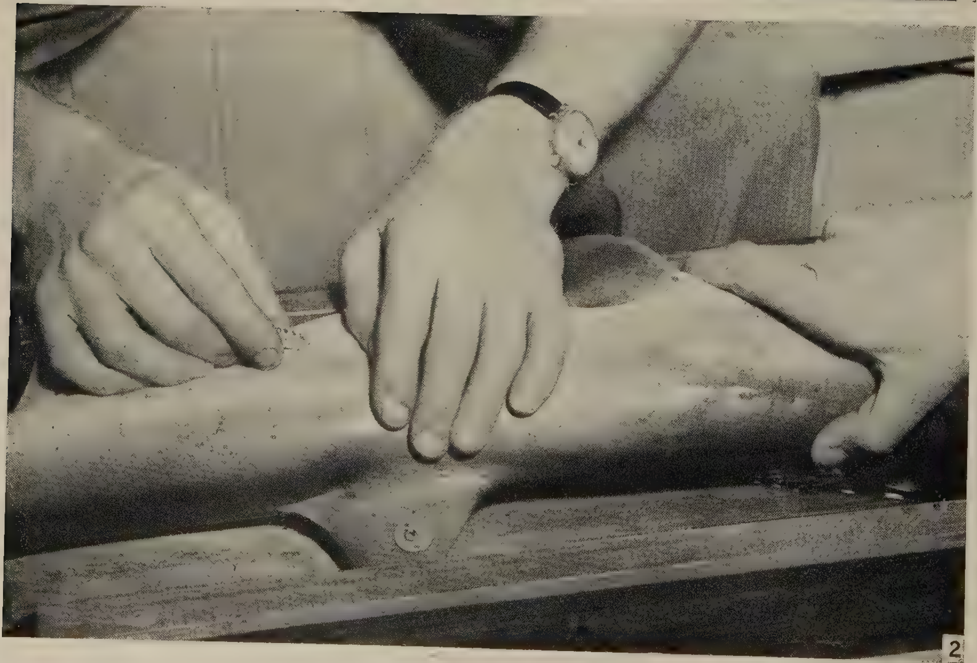

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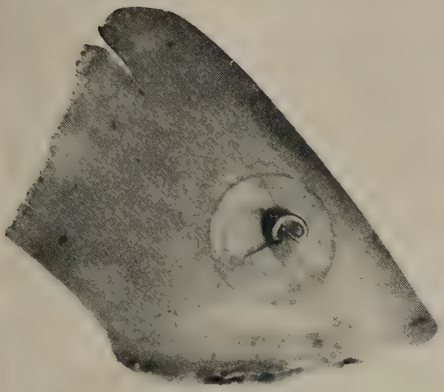
PLATE 3

TAGGING OF SCHOOL SHARK



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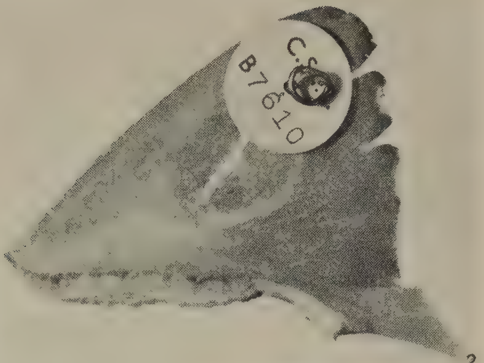

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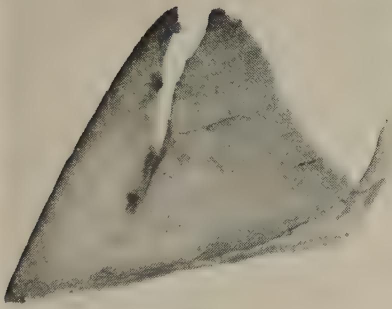

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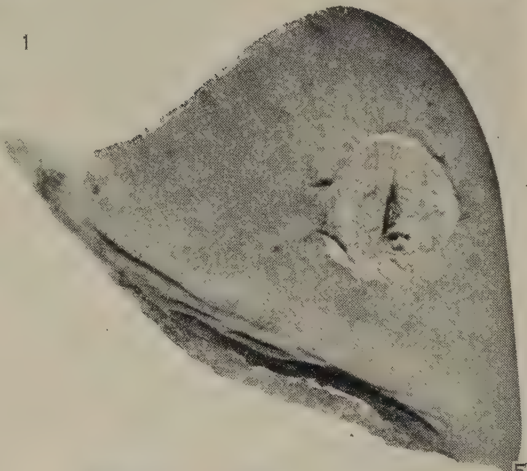

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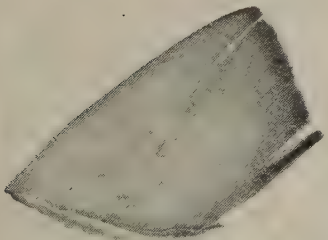

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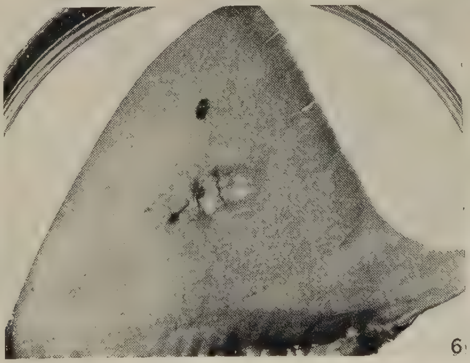

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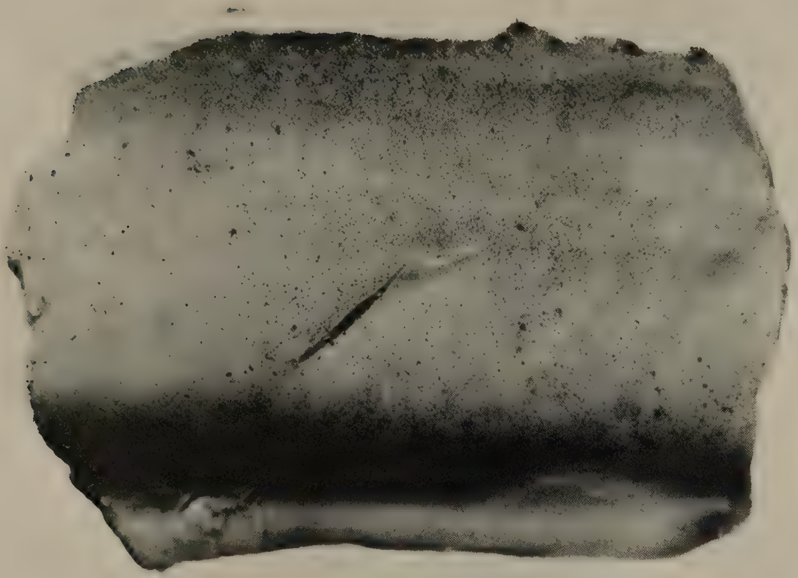
TAGGING OF SCHOOL SHARK



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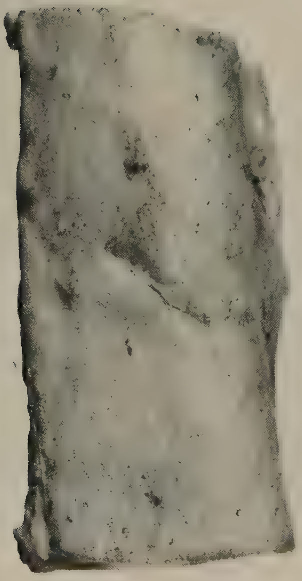

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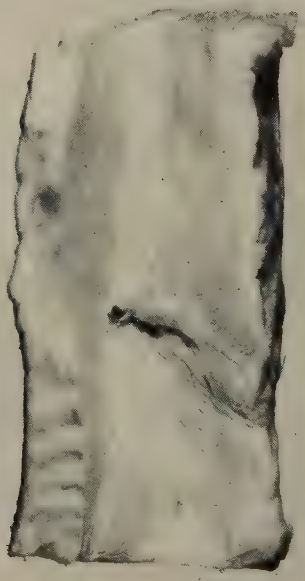

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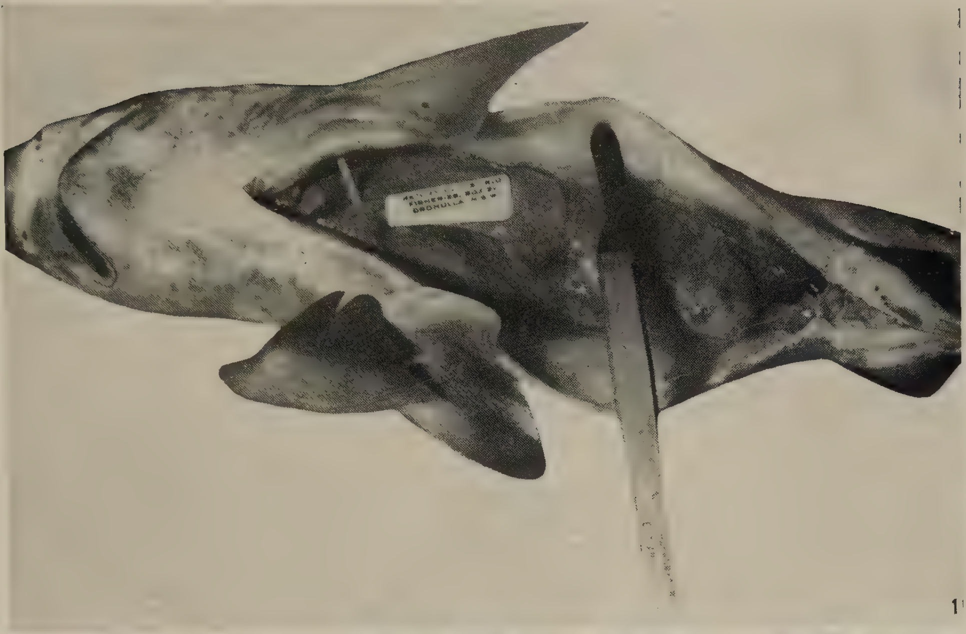

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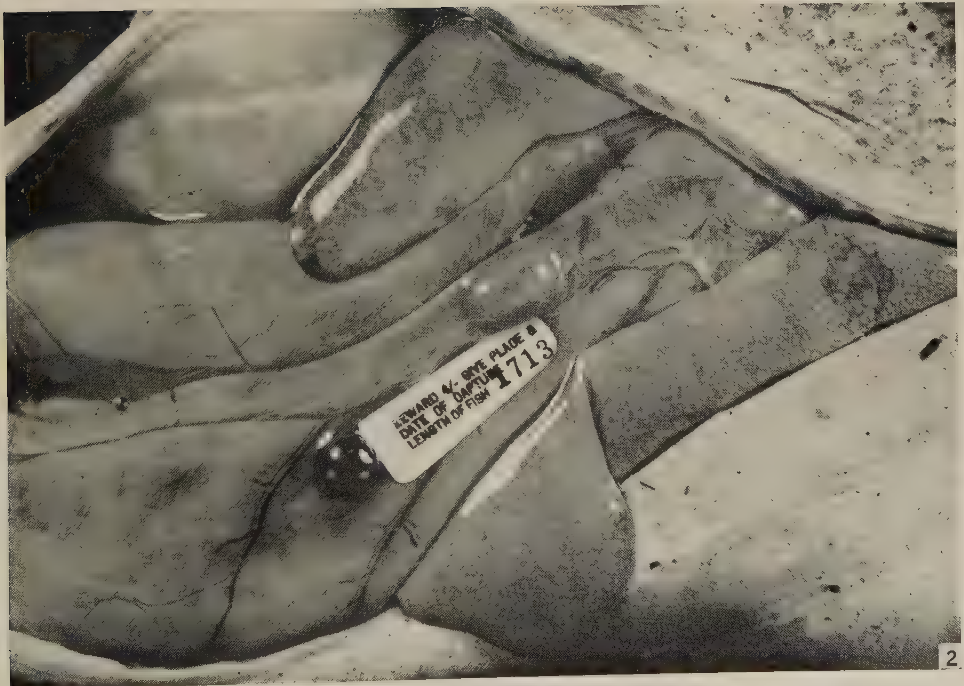

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2

INTERTIDAL ZONATION OF THE EXPOSED ROCKY SHORES OF VICTORIA, TOGETHER WITH A REARRANGEMENT OF THE BIOGEOGRAPHICAL PROVINCES OF TEMPERATE AUSTRALIAN SHORES

By ISOBEL BENNETT* and ELIZABETH C. POPE†

(*Manuscript received April* 24, 1952)

Summary

This paper continues previous ecological studies (Dakin, Bennett, and Pope 1948) of the intertidal zone of south-eastern Australia.

The environmental factors and the zonation of the animals and plants on the exposed rocky coasts of Victoria are described.

As a result of this survey a rearrangement of the biogeographical provinces of the Australian littoral is made, and a new *Cool-temperate* fauna and flora are recognized on the coast of Victoria.

I. INTRODUCTION

This paper describes a further section of the ecological and biogeographical survey of the intertidal zone begun in 1945 on the shores of New South Wales (Dakin, Bennett, and Pope 1948), and now extended south and west to include the Victorian coast. Certain conclusions are drawn which necessitate a rearrangement of the biogeographical provinces of temperate Australian shores.

Serious illness prevented Professor Dakin from taking part in active field work, but many of the field expeditions were planned and supervised by him and his suggestions and notes were used in preparing this account. Whilst his name must, therefore, be closely associated with the work, the present authors should be held entirely responsible for any opinions expressed.

In a review of the previous paper, Stephenson (1950) regretted that scant attention had been paid to the biogeographical implications of the survey. The time was not then opportune for such a discussion, because very little was known about intertidal zonation in Victoria, only one or two very restricted localities in South Australia had been described, and there was practically no modern information available for Western Australia. Whilst systematic accounts existed for some of the marine groups in Victoria (Bale 1889; Clark 1946; Cotton and Godfrey 1938; Gabriel 1936; Gatliff 1887, 1888; Harvey 1858-63; Hubendick 1946; Macgillivray 1887; Macpherson and Chapple 1951), and a survey of the flora and fauna of Julia Percy I. (lat. 38° 21′ S., long. 141° 36′ E.) had been

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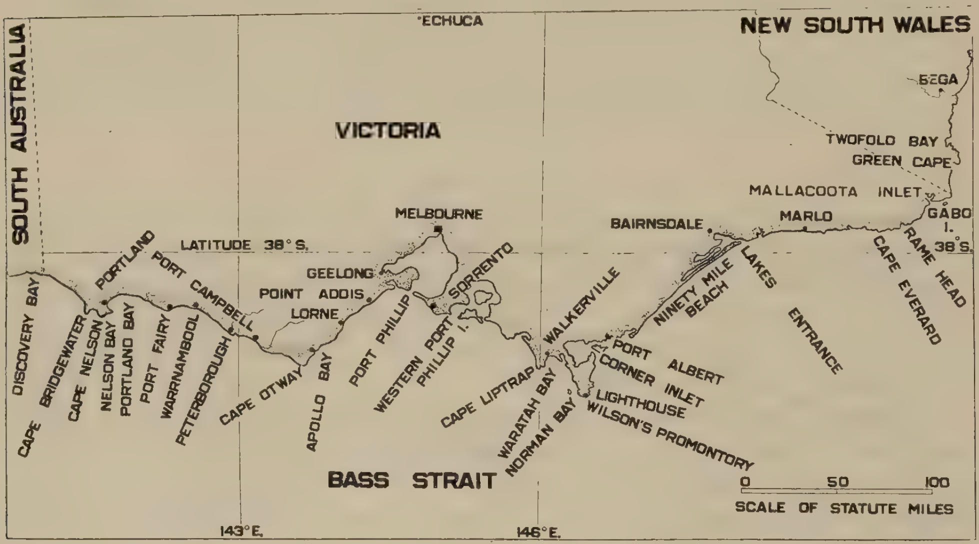
† Australian Museum, Sydney. By permission of the Trustees.

made by the McCoy Society (1937), no mention could be found in literature of the broader aspects of shore ecology.

Stephenson (1948, p. 211) had issued warnings against the dangers of basing statements about geographical provinces on such sources as check lists or unreliable systematic accounts which, as a rule, give no true picture of the mode of occurrence of a species, or of its relative abundance and importance.

With the object of obtaining the necessary data four field expeditions were made between March 1949 and February 1951 when the authors were accompanied and greatly assisted by two members of the staff of the National Museum of Victoria, Miss J. H. Macpherson and Mr. C. W. Brazenor.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ECHUCA
NEW SOUTH WALES
BEGA
VICTORIA
TWOFOLD BAY
GREEN CAPE
MALLACOOTA INLET
GABO I.
MARLO
BAIRNSDALE
MELBOURNE
LATITUDE 38° S.
38°S.
PORTLAND
PORT CAMPBELL
GEELONG
POINT ADDIS
LORNE
SORRENTO
DISCOVERY BAY
CAPE BRIDGEWATER
CAPE NELSON
NELSON BAY
PORTLAND BAY
PORT FAIRY
WARRNAMBOOL
PETERBOROUGH
CAPE OTWAY
APOLLO BAY
PORT PHILLIP
WESTERN PORT
PHILLIP I.
CAPE LIPTRAP
WALKERVILLE
WARATAH BAY
NORMAN BAY
PORT ALBERT
CORNER INLET
LIGHTHOUSE
WILSON'S PROMONTORY
NINETY MILE BEACH
LAKES ENTRANCE
CAPE EVERARD
RAME HEAD
BASS STRAIT
0
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100
SCALE OF STATUTE MILES
143°E.
146°E.

Fig. 1.—Map of the Victorian coast showing places mentioned in text.

For the present survey, methods similar to those employed on the coast of New South Wales were used but were somewhat hampered by prevailing rough seas. It was not possible to make exhaustive collections during the present survey, but since this was not primarily concerned with the rarer species, the collections satisfactorily represent the commoner and ecologically prominent animals and plants.

In all, 16 points along the Victorian coast were visited, from Bastion Point, Mallacoota (just west of Gabo I.) in the east, to Cape Bridgewater in the west (Fig. 1). The only area of coast not examined by the authors either in the present or previous survey, is the section between Mallacoota Inlet and Port Albert. Since this includes over 100 miles of continuous sandy beach (with which this report is not concerned), the gap in the records is negligible.

In setting out the results of this survey, the biota of the intertidal zone of the Victorian coast is described, and then the biogeography of the temperate parts of the Australian coastline is discussed.

Terminology

Womersley and Edmonds (1952) criticized some of the terms used by Stephenson and Stephenson (1949). In the present work the latter authors have been followed except in their use of the term "mid-littoral".

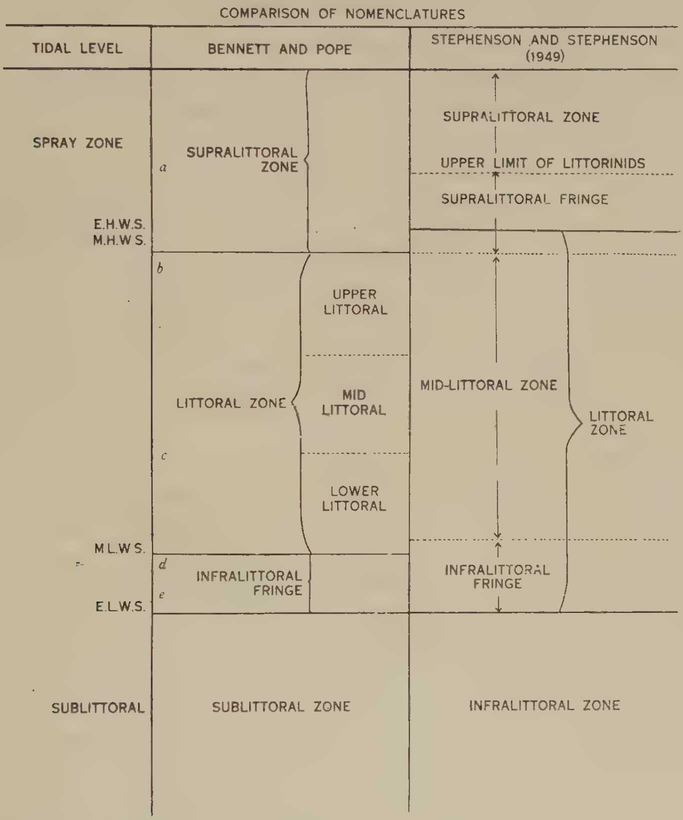
COMPARISON OF NOMENCLATURES
TIDAL LEVEL
BENNETT AND POPE
STEPHENSON AND STEPHENSON (1949)
SPRAY ZONE
E.H.W.S.
M.H.W.S.
M.L.W.S.
E.L.W.S.
SUBLITTORAL
a
SUPRALITTORAL ZONE
b
UPPER LITTORAL
LITTORAL ZONE
MID LITTORAL
c
LOWER LITTORAL
d
INFRALITTORAL FRINGE
e
SUBLITTORAL ZONE
SUPRALITTORAL ZONE
UPPER LIMIT OF LITTORINIDS
SUPRALITTORAL FRINGE
MID-LITTORAL ZONE
LITTORAL ZONE
INFRALITTORAL FRINGE
INFRALITTORAL ZONE

Fig. 2.—Relationship between terms used in the present paper and those proposed by Stephenson and Stephenson (1949). In Allee *et al.* (1949) the term "eulittoral" is used where the Stephensons use "littoral". It is felt that the former may be preferable.

E.H.W.S. = Extreme high water mark of springs.
M.H.W.S. = Mean " " " " "
M.L.W.S. = Mean low " " " "
E.L.W.S. = Extreme low " " " "

As Womersley and Edmonds have pointed out, it is cumbersome to designate subdivisions such as upper, mid, and lower sections of a "mid-littoral" area, and this is often desirable on the wide rock platforms which characterize southern Australian shores. Figure 2 correlates the terms used by Stephenson and Stephenson with those in the present work.

II. The Intertidal Biota of the Victorian Coast

(*A*) *Environment*

(i) *Substratum*

The physiography of various parts of the Victorian coast has been described by Bartrum (1926), Ongley (1940), Gill (1943), Baker (1944), Hills (1946), and Jutson (1949).

The rocky outcrops included Devonian sandstones and slates (Bastion Point, Mallacoota), granites (Wilson's Promontory), basalts (Phillip I.), Jurassic sandstones (Lorne), Miocene limestone (Port Campbell), and consolidated dune limestones (Warrnambool). Only in a few instances has weathering produced the wave-cut rock platform characteristic of much of the central New South Wales coast. Examples occur near The Nobbies, Phillip I.; at Walkerville on Waratah Bay; Sorrento; Point Addis; and at Lorne and Apollo Bay (Plate 2, Fig. 2; Plate 4, Fig. 1). The intertidal zone is often a narrow band, either on a vertical face or on a narrow bench as in the limestones of the Port Campbell district (Plate 5, Fig. 1) or on steeply sloping turtle-backs of rock as at Cape Bridgewater (Plate 5, Fig. 2) or Wilson's Promontory (Plate 1).

At certain places, from Peterborough to Warrnambool, a series of terraces of moderate extent were noted in the dune limestone, the upper ones being intertidal and the lower ones below the lowest tides.

For long stretches of the open coast, notably from the Bay of Islands at Peterborough to Port Campbell, sandy beaches are mostly small or absent, and a succession of vertical cliffs, with narrow benches at their base, face the ocean (Plate 5, Fig. 1). In most other areas on the south-east coast of the continent, sandy beaches alternate with rocky headlands.

The complexity of the intertidal animal and plant communities varied greatly with the shelter, slope, aspect, and degree of weathering of the rocks, although the actual differences in chemical composition of the substratum, including the limestones, had little or no effect on the general pattern of zonation.

(ii) *Hydrographic and Climatic Conditions*

No hydrographic or climatic data have been published for the intertidal zone of the exposed Victorian coast and the literature on coastal waters is scanty. The little that is known is summarized below, being the only data available to the present authors. It is stressed, however, that such data apply to the area of shipping lanes or to coastal weather stations rather than to the intertidal zone. It would be foolhardy to deduce from these data conditions in the intertidal zone since these latter vary so greatly with local conditions. The data do indicate broadly how Victorian seas and shores differ from those of the coast of New South Wales and the adjacent coast of South Australia.

Literature and sources of data.—Dannevig (1907, 1915) wrote of the currents and tidal streams in Bass Strait and based his findings on direct observations. Riddle (1920) published a map of the currents round Australia and Halligan (1922, 1930) published temperature data and a map of the currents. Papers by David (1932) and David and Browne (1950) contained maps of sea currents but added no new facts, merely adapting information from other workers.

Tidal information has been published by Chapman (1938) and additional information was obtained from the Tide Tables issued annually by the Ports and Harbours Branch of the Victorian Department of Public Works. Much of the above data is reviewed by Macintosh (1949).

Two important sources of data were the series of charts issued by the Royal Netherlands Meteorological Institute (1949) and Volume IV of the C.S.I.R.O. Oceanographical Station List (1951). Additional sources used were temperature records supplied by Dr. Anton Bruun (Danish Deep-sea Expedition 1950-52), and records of the Victorian Branch of the Commonwealth Meteorological Bureau. These are summarized below:

(1) *Sea Temperatures.*—Surface temperatures off the Victorian coast were obtained from records from literature, and from the Danish Deep-sea Expedition 1950-52.

All records from such sources as Navy hydrographic offices, charts, and literature issued before 1949 have been neglected here since the best of world data have been summarized in the series of charts published by the Royal Netherlands Meteorological Institute (1949). From these charts it is clear that the Victorian coastal waters are consistently at least 2-3°C. lower in temperature than those bathing the adjacent coasts of New South Wales or South Australia. The average summer temperatures off Victoria lie between 16 and 19°C. and winter ones average between 12 and 13°C. The average of the maxima recorded for more than 50 years is 17.6°C. and that of the minima 11.8°C. Another interesting fact recorded in the Dutch charts is that the stretch of coast from Cape Otway west to approximately the South Australian border is the coldest region of the Victorian coast during the warmer months of the year. This will be referred to later.

Further important data for the years 1949-50 are to be found in C.S.I.R.O. Oceanographical Station List, Vol. IV (1951) for a station at latitude 38° 22′ S., longitude 144° 36′ E. off Port Phillip Heads. Maximum surface temperature recorded was 19.6°C. (in December) and the minimum 11.7°C. (in July) but since these records were made at irregular and sometimes more than monthly intervals, the true maxima and minima may have been missed. Also, since the station cannot altogether be considered to lie outside the area influenced by the waters of the large, shallow bay, Port Phillip, these C.S.I.R.O. figures cannot be taken as representative of the whole of Bass Strait. Danish data have shown the temperatures in the Port to be nearly 2°C. warmer in summer than those in Bass Strait.

However, it is clear that sea temperatures along the Victorian coast are significantly lower by at least 2-3°C. than would normally be expected at that latitude. Figure 3, adapted from Rochford (1951) shows the annual mean surface temperatures during 1949 for a series of onshore stations on the coast of New South Wales, one station in Bass Strait, and two stations on the east coast of Tasmania plotted against latitude. In it the water temperatures off the Victorian coast are seen to parallel those off southern Tasmania and therefore to be unexpectedly low.

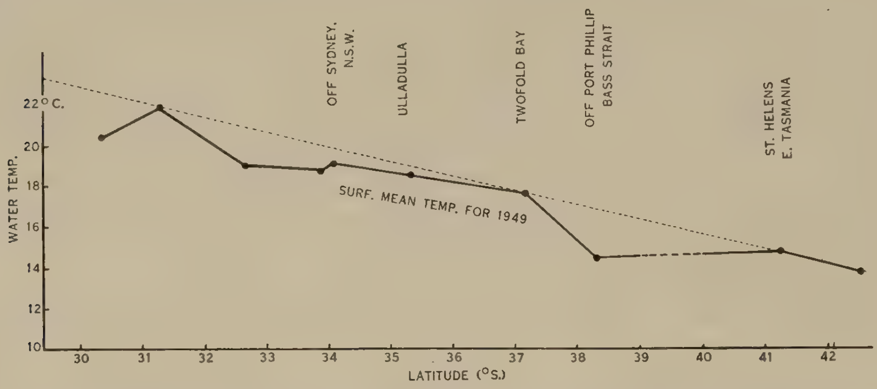

Fig. 3.—Surface annual mean of temperature of neritic waters during 1949 along the eastern Australian coastline and in Bass Strait. The dotted line represents a normal meridional trend in the absence of up-welling. (Adapted from Rochford.)

Direct evidence of the body of colder water along the Victorian coast was furnished by data from the records of the Danish Deep-sea Expedition 1950-52, and is set out in Table 1.

Table 1 shows a marked drop of more than 3°C., with observations beginning between Tuross Heads and Green Cape in New South Wales. From here, along the Victorian coast, the temperature continued to fall till, off South Australia, near Kangaroo I., it rose again markedly. During the return journey of the *Galathea* through Bass Strait the same phenomenon was recorded.

All temperature records show the same tendency. Readings off the Victorian coast are significantly lower than those off the adjacent coasts of South Australia and New South Wales. Sea temperatures are, in fact, comparable to those of southern Tasmanian waters.

Stephenson (1948, p. 215) selected 10°C. (winter sea temperature) as the approximate barrier dividing warm- and cool-temperate provinces. According to this theory Victorian seas should support a warm-temperate biota, for the average winter minimum, according to available data, is

11.8°C. In Section II (*B*) it is shown that this is not so, and the cool-temperate component is dominant in the Victorian intertidal zone.

It is stressed again that *intertidal* temperatures may well differ from those quoted above and therefore they may be lower in winter and fit in Stephenson's theoretical range. If this is not so, Stephenson's 10°C. limit may have to be altered to a slightly higher figure.

(2) *Currents.*—Detailed monthly analyses of currents round Australia have been published as a series of charts by the Royal Netherlands Meteorological Institute (1949). These show that there is no prolonged or sustained current bathing the Victorian coast. As Dannevig (1915) stated Bass Strait is an area where circulation of the waters is complex.

TABLE 1

TEMPERATURE READINGS IN SOUTH-EASTERN AUSTRALIAN WATERS MADE BY H.D.M.S. "GALATHEA"

Date	Hour	Position		Temperature (°C.)
		Lat.	Long.	
2.xii.1951	1710	36°00′S.	150°31′E.	19.30
,,	2310	37°20′S.	150°15′E.	16.19
3.xii.1951	0720	38°00′S.	149°38′E.	15.33
,,	1510	38°20′S.	148°48′E.	14.82
,,	2310	38°40′S.	147°50′E.	13.70
4.xii.1951	0715	39°08′S.	147°50′E.	14.75
,,	2300	38°50′S.	142°30′E.	15.13
5.xii.1951	0845	38°00′S.	139°28′E.	14.70
,,	1500	38°00′S.	139°23′E.	15.84
6.xii.1951	0245	37°11′S.	138°41′E.	15.92
,,	1515	36°00′S.	138°54′E.	18.34

Most authors and charts, except Dannevig (1907), have shown strong currents from west to east, flowing along the Victorian coast throughout the year. The Dutch charts with monthly statistical analyses demonstrate that this is not so. In fact currents are variable from September to April, and from May to August only is there a slight predominance of currents from the west. This current is only marked in Bass Strait and along the Ninety Mile Beach. To the west of Cape Otway, however, during the colder months currents are variable and occasionally flow onshore from the south. The Dutch charts also show that nothing is known of the inshore currents round the Great Australian Bight and that it is impossible to know whether the current flows from west to east along this coast or whether, as depicted by some authors, there is a counter-current flowing west. The only constant current is the Tasman or Notonectian current flowing south down the east coast of New South Wales. This flows strongly close to the coast as far south as Cape Howe before swinging offshore in the warmer months (September to April) but in the colder months it swings offshore farther north at Cape Hawke and is weaker to the south of this point.

(3) *Wind and Waves.*—Winds with a westerly component prevail on the Victorian coast in that they blow for a slightly higher percentage of the year than any other. During the summer months, however, southerly winds prevail west of Cape Otway and in Bass Strait. Both westerly and southerly winds are cold.

Many of the stormy conditions and high seas round Wilson's Promontory (in the east) and also west of Cape Otway (in the west) are produced under the influence of the westerly winds but severe storms may also come from the east.

No records exist of the size of breakers on Victorian shores but the seas there have the reputation of being rough and the present authors' experience of them certainly agreed with this. For instance, in the Portland area, when there were no white-capped waves at sea, breakers surged 50-100 ft. up the cliffs.

(4) *Tides.*—Tidal conditions are more complicated than in New South Wales. Leaving aside the bays and inlets, the spring tidal ranges vary between 9 ft. at Wilson's Promontory and approximately 3 ft. in the Portland to Warrnambool area. This difference has little effect on the intertidal zonation of the plants and animals except to reduce the absolute vertical heights of the bands of dominant organisms where the tidal range is less (Section II (*B*) (i)).

In the east of Victoria, tides are semi-diurnal but in the Portland area they are irregular. According to the tide tables they remain semi-diurnal for a period of a week or several weeks and then, for a varying number of days, there may be only one high and one low tide in the 24 hours ("Dodger tides", Chapman 1938). This irregular behaviour has no marked effect on the zonation of organisms in western Victoria.

(5) *Air Temperatures.*—Records of the temperatures kept by the weather stations at Wilson's Promontory, Cape Otway, Warrnambool, and Portland show only slight differences in temperatures. The maxima recorded in 1951 vary from 21.5°C. in the east to 25.2°C. west of Cape Otway. The minima for that same year range from 7.1 to 10°C., both these being recorded west of Cape Otway.

Average maxima over long periods of years (up to 66 years) lie round about 21.67°C. from Cape Otway westwards, and 20.1°C. at Wilson's Promontory. It must not be forgotten, however, that occasional hot days with temperatures over 38.0°C. may occur exceptionally in Victoria. Mean minimum temperatures over similar long periods have ranged from 6.11°C. at Warrnambool to 7.8°C. at Wilson's Promontory.

(6) *Humidity.*—Owing to prevailing rough seas, the amount of wind-blown spray was generally very high and the impression was gained that desiccation would be much less severe than on the New South Wales coast.

Summary of Environmental Conditions.—The Victorian coast is bathed by seas which are generally colder by 2-3°C. and probably as much as 3-5°C. than those in New South Wales and in the Flindersian Province west of Kangaroo I., South Australia. The intertidal zone is more heavily wave washed than in New South Wales and air temperatures are, on the whole, lower. Salinities have not been dealt with since they are reckoned to have little importance in this instance.

(*B*) *Zonation of the Exposed Rocky Coast of Victoria*

(i) *Basic Zonation*

Figure 4 shows diagrammatically the zoning patterns of four sections of the Victorian coast—two in the eastern section at Bastion Point, Mallacoota, and Wilson's Promontory; one typical of the central area of the coast, at Lorne; and one typical of conditions in the extreme west of the State, at Nelson Bay. A fifth zoning pattern, typical of the coast of New South Wales, is included for comparison. Exposure is submaximal in all these localities except Wilson's Promontory where it is maximal and where the effect is a reduction of the mussel beds in the middle area of the littoral and a great development of the barnacles.

In spite of the differences between the four Victorian localities, a common basic pattern may be recognized. There are five major zones:

(*a*) *The* Melaraphe-*lichen zone* in the supra-littoral area.

(*b*) *A wide barnacle-mussel zone* which occupies the middle and upper part of the littoral. The prominent cirripedes are *Chamaesipho columna** and *Catophragmus polymerus*, with *Chthamalus antennatus* also present in the east of the State and as far west as Cape Otway. The mussel species which characterize this part of the littoral are *Brachyodontes rostratus, Modiolus pulex,* and occasionally *Mytilus planulatus* in Victoria, with the addition in the southern waters of Bass Strait of *Brachyodontes erosus,* which occurs on the shores of islands in the Furneaux Group. It should be noted that Fischer (1940, footnote p. 309) considers both *B. erosus* and *B. rostratus* as synonymous with the Red Sea species, *B. variabilis* Krauss.

(*c*) According to the degree of shelter, the next zone is marked either by the presence of a mixed algal community in exposed places or by encrustations of tubes of the serpulid, *Galeolaria caespitosa,* in less exposed places.

(*d*) A somewhat "bare" area of rock that has this appearance because it is populated either by inconspicuous close-growing species such as 'lithothamnion' or because such other organisms as are present grow more widely separated one from the other than in New South Wales. For example, at certain places the ascidian *Pyura stolonifera*† is found in this

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* Authors of the scientific names omitted in text are given in list Section II (*b*)(iii).

† = *Pyura praeputialis* (Heller)—Dakin, Bennett, and Pope 1948.

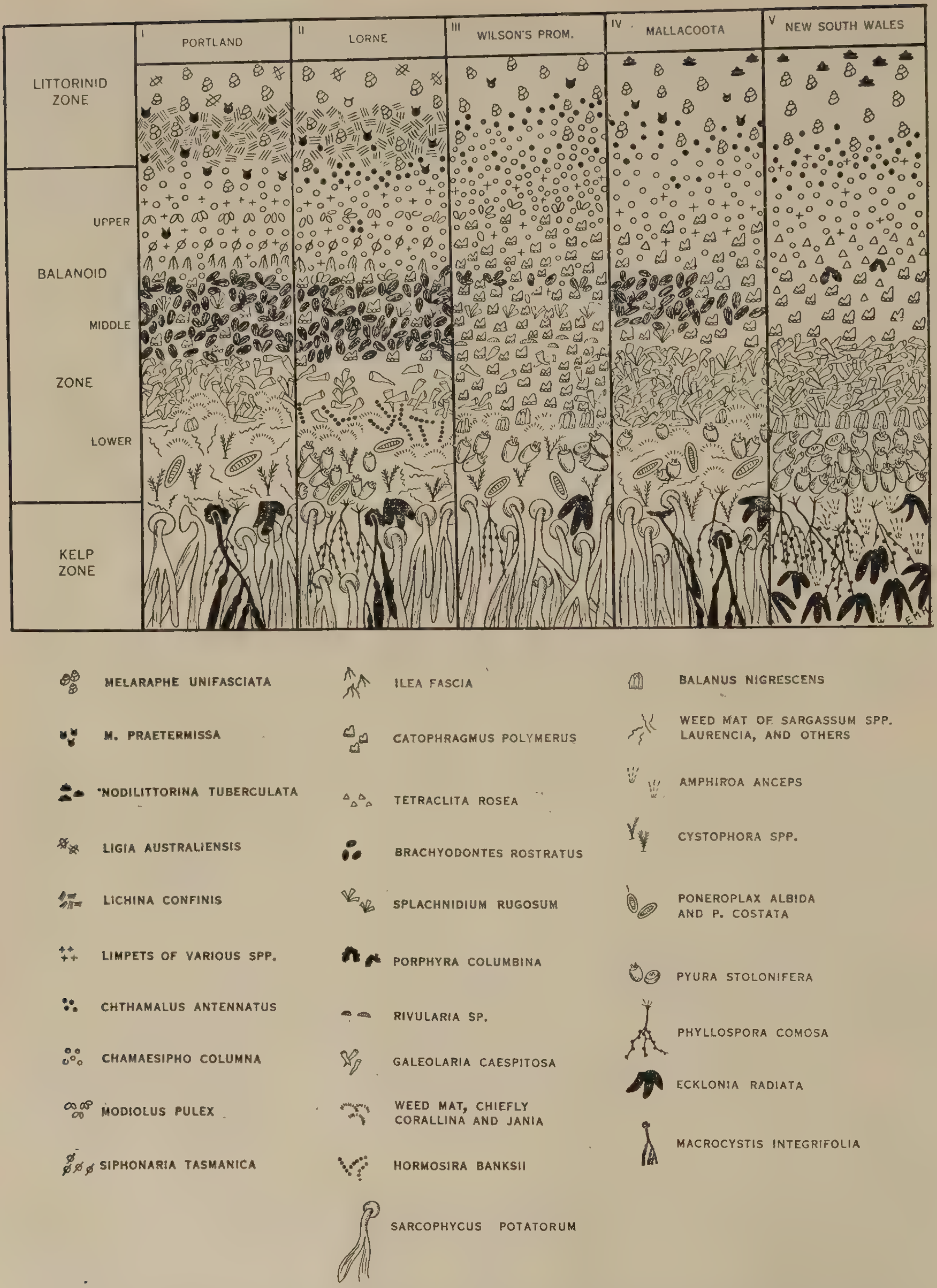
I PORTLAND
II LORNE
III WILSON'S PROM.
IV MALLACOOTA
V NEW SOUTH WALES
LITTORINID ZONE
UPPER
BALANOID
MIDDLE
ZONE
LOWER
KELP ZONE
EHR
MELARAPHE UNIFASCIATA
M. PRAETERMISSA
NODILITTORINA TUBERCULATA
LIGIA AUSTRALIENSIS
LICHINA CONFINIS
LIMPETS OF VARIOUS SPP.
CHTHAMALUS ANTENNATUS
CHAMAESIPHO COLUMNA
MODIOLUS PULEX
SIPHONARIA TASMANICA
ILEA FASCIA
CATOPHRAGMUS POLYMERUS
TETRACLITA ROSEA
BRACHYODONTES ROSTRATUS
SPLACHNIDIUM RUGOSUM
PORPHYRA COLUMBINA
RIVULARIA SP.
GALEOLARIA CAESPITOSA
WEED MAT, CHIEFLY CORALLINA AND JANIA
HORMOSIRA BANKSII
SARCOPHYCUS POTATORUM
BALANUS NIGRESCENS
WEED MAT OF SARGASSUM SPP. LAURENCIA, AND OTHERS
AMPHIROA ANCEPS
CYSTOPHORA SPP.
PONEROPLAX ALBIDA AND P. COSTATA
PYURA STOLONIFERA
PHYLLOSPORA COMOSA
ECKLONIA RADIATA
MACROCYSTIS INTEGRIFOLIA

Fig. 4.—Diagrammatic representation of the principal zoning organisms in the inter-tidal zone in south-eastern Australia. A key to the meaning of the symbols is appended. In all but column III exposure is submaximal. Tidal ranges varied between 4 and 9 ft. but for this diagram the zoning patterns have been based on a norm with a tidal range of 6 ft. and the various zones are reduced or enlarged to occupy the same proportional width of the tidal range as they do on the shore.

zone, but only east of Cape Otway, and except at Norman Bay, Lorne, and Apollo Bay, is very much sparser than in New South Wales.

Large chitons of the genus *Poneroplax* are often the markers of this zone when *Pyura* is absent. It is also on this level of the shore that a number of the species of the alga *Cystophora* are found, e.g. *C. torulosa, C. intermedia, C. paniculata, C. retorta, C. siliquosa,* etc.

(*e*) A zone of large brown algae in which the giant brown fucoid, *Sarcophycus potatorum*, is the dominant species, often accompanied at a lower level by the kelp *Macrocystis integrifolia.*

In Figure 2, the small letters in column 2 mark the upper limits of these zones.

(*a*) *The* Melaraphe-*lichen Zone.*—The organisms characterizing the supra-littoral zone in Victoria may cover a wide vertical expanse of rocks, especially in the west, where the continual presence of fine, wind-blown spray or even drops of water from the breaking of high seas keeps the atmosphere moist. At Cape Nelson, for instance, the crabs *Cyclograpsus audouinii* and *Brachynotus octodentatus* were found in wet places among the grass and boulders 40-50 ft. above sea-level, and *Paragrapsus gaimardii* occurred not far below. A number of other crustaceans, amphipods (*Talorchestia ? diemenensis*), and isopods were also found at this height. *Ligia australiensis* was the commonest isopod—occurring in thousands—especially if there were sheltering boulders at high shore levels. Its presence was noted by the authors between Lorne and Cape Bridgewater on the open coast, and it has been recorded by Edmonds (1948) at Kangaroo I. East of Lorne it was not found in this situation, but probably, as in New South Wales, it abounds in the bays and inlets. At Long Reef near Sydney, the crab *Cyclograpsus audouinii* and an amphipod, *Talorchestia novae-hollandiae,* have been recorded in the high supra-littoral, but whereas the crab is somewhat rare on the coast of New South Wales, it is common in Victoria. The crabs *P. gaimardii* and *B. octodentatus* do not occur generally on the east coast of the continent, but they have been recorded by Tweedie (1942) from Tasmania. The present authors collected *B. octodentatus* on the open coast between Cape Bridgewater and Lorne but not east of this point.

At a lower level, but still in the supra-littoral, occurs a large population of littorinid molluscs of the species *Melaraphe unifasciata* and *M. praetermissa.* Whilst the former occurs throughout the temperate coasts of the continent, *M. praetermissa* is found only between Mallacoota Inlet in the east and Cape Bridgewater in the west in Victoria, and on Tasmanian shores. It is not recorded at Kangaroo I. (Edmonds 1948).

Where the two littorinid species occur together, *M. unifasciata* is found higher up than *M. praetermissa,* but their vertical distributions overlap considerably. Conditions of increased shelter seem to favour *M. praetermissa,* which is commoner in Nelson Bay than *M. unifasciata,* whilst on the neighbouring exposed cape the latter species is in the ascendancy.

A third species of littorinid, *Nodilittorina tuberculata*, is found with the two *Melaraphe* species at Bastion Point on the extreme east coast of Victoria, but this appears to be the southern limit of its range. It is not therefore a typical inhabitant of the Victorian supra-littoral.

One marked feature of the Victorian supra-littoral is the presence of a dark band of lichens. The lichen at Walkerville, Waratah Bay (Plate 3, Fig. 1) has been identified by the National Herbarium, Melbourne, as *Lichina confinis*, and it grows in the littorinid area where the ranges of the two species overlap. Occurring in a similar way at Warrnambool and Nelson's Bay near Portland is a *Verrucaria* provisionally identified by H. B. Womersley as *V. microsporoides*. This dark band of lichens was missing at Wilson's Promontory on the smooth granite rocks, but was present from immediately west of this point to Portland, and also to the east of it, where it occurred sporadically, so that it may be considered a regular feature of the Victorian coast.

In the lower part of the supra-littoral, an occasional carnivorous gastropod, *Lepsiella vinosa*, and the limpet *Patelloida latistrigata* occur, although they are more numerous in the next zone.

(*b*) *The Barnacle-mussel Zone.*—This zone occupies the upper and middle portions of what Stephenson and Stephenson (1949) define as the balanoid zone. The upper limit of this zone is pushed higher up the shore in areas constantly subjected to wave action, and in addition the conformation of the intertidal rocks can cause widening of this zone, as can an increasing tidal range.

The best development of an intertidal barnacle zone, both from the point of view of population density and the width of the zone, was observed at Wilson's Promontory near the eastern landing place for the lighthouse (Plate 1). Here the favourable conditions appear to be: (1) the constant surge, (2) the smooth-surfaced, hard, red granite rocks which slope from low-water level at an angle which allows each wave to wash up the rocks to a great height, and (3) the comparatively greater tidal range on this part of the Victorian coast. Here the rocks were covered for a vertical height of 11 ft. or more with barnacles so closely packed that it was difficult to see the rock between them. Another very well-developed barnacle zone was seen at Hayley's Reef, just offshore at Apollo Bay. Apart from these two exceptional places there were, on the whole, fewer barnacles per unit area in Victoria than in similar areas in New South Wales. *Chthamalus antennatus* was absent along the 200 miles of coast to the west of Cape Otway but it is reported to occur in its usual habitat, high up on the shore, in South Australia.

In a paper on the intertidal ecology of the Freycinet Peninsula, in Tasmania, Guiler (1951, p. 68) tentatively suggests that the red granite substratum is unsuitable for intertidal organisms and particularly barnacles. Our findings at Wilson's Promontory, where the same red granite occurs, do not support this view.

Different species of barnacles are dominant at different levels generally as follows, from the top of the zone seawards: *Chthamalus antennatus* (but only east of Cape Otway), *Chamaesipho columna*, and *Catophragmus polymerus*. *Balanus nigrescens* occurs lower on the shore than any of these species (see (*d*) below). The relative positions of these barnacles may be seen in Figure 4, column III.

Considerable overlapping occurs in the vertical ranges of the adjacent species of the three first mentioned above, but only rarely (e.g. at Wilson's Promontory) does the vertical range of *Catophragmus* overlap that of *Chthamalus*.

Another species of barnacle, *Tetraclita rosea*, may be present along with *Catophragmus* on exposed rocks but it has only been recorded in the far eastern corner of the Victorian coast. It ranges north up to Queensland. Towards the southern end of New South Wales it is very scarce and whilst a few scattered specimens were observed at Bastion Point, Mallacoota, none could be found at Wilson's Promontory. This absence is one of the conspicuous differences between the corresponding zones in the two States.

At Cape Bridgewater, in the west, where exposure to wave action and cold temperatures (both during winter and summer) is greatest, *Catophragmus* was scarce or absent. Where this occurred, *Chamaesipho columna* took over and colonized the lower level of the zone, thus occurring much lower than previously recorded, and extending down to the mixed algal zone.

Superimposed on this somewhat simple arrangement of barnacles are a series of bands of algae, or of animals such as limpets, siphonarias, periwinkles or, most noticeable of all, a band of mussels. In suitable localities, the mussels may even oust the barnacle *Catophragmus* and relegate it to a position of secondary importance, as for instance at Lorne where *Brachyodontes rostratus* covers a wide area of rock to the virtual exclusion of most other species, and the few individuals of *Catophragmus* present are attached to the mussel valves (Plate 4, Figs. 1, 2; Plate 6, **Fig. 1**).

Some of the bands mentioned above may be seasonal, such as that of the alga *Splachnidium rugosum* which is prominent during summer in the area where *Catophragmus* occurs. A well-developed band was present in May at Wilson's Promontory, but it was absent 5 months later. This alga appears as the lower of two dark bands in Plate 1, Figure 1. The upper dark band shows where mussels occur along with the barnacles.

Columns I-IV in Figure 4 show the prominent associated species in the Victorian barnacle zone. Among these are the algae *Ilea fascia*, *Rivularia firma*, and *Splachnidium rugosum*. *Ilea fascia* is probably seasonal and was only a dominant zoning organism along the western half of the Victorian coast whilst *Rivularia firma* was found only in the east. The mode of occurrence and the heights relative to the various species of barnacle at which these algae occur are shown in Figure 4.

Among the more prominent associated animals in the barnacle zone are the mussels *Brachyodontes rostratus, Modiolus pulex,* and more occasionally in Victoria, *Mytilus planulatus.* The last occurs sporadically on the exposed Victorian coast, but is evidently more frequently found in such situations in Tasmania (Guiler 1951). It occurs in sheltered waters in Victoria.

Mussel bands are best developed on coasts which, while exposed to surf, are sheltered to some extent from the worst of heavy seas. For instance, *Brachyodontes rostratus* occurs sparsely and only under overhanging boulders or in crevices at Cape Bridgewater or on Phillip I. In Waratah Bay at Walkerville, or on the wider rock platforms at Lorne and Apollo Bay, the mussel band reaches its best development. Plate 4 shows well-developed beds of *Brachyodontes* and indicates their density. As many as 2080 individuals were counted in a square foot at Nelson Bay (Plate 6, Fig. 1), and 424 full-sized *Brachyodontes* (juveniles neglected) occurred in the same area at Lorne. Here wide areas of rocks were populated by the mussels (Plate 4, Fig. 1) and those *Catophragmus* barnacles present were growing on the mussel shells in the upper two-thirds of the latter's range. The largest mussels were found constantly in the middle area of their vertical ranges. These were 4 ft. at Walkerville in the east, and 2 ft. at Nelson Bay in the west (where the tidal range is half that in the east), so that the band of mussels occupies throughout Victoria approximately the same proportional height in the tidal range.

The Brachyodontes *association.*—The shelter provided by the mussels affords a habitat for an association of species including as constant elements: a species of polyclad near *Leptoplana australis,* a green nereid worm, a red anemone *Actinia tenebrosa,* the stalked barnacle *Ibla quadrivalvis,* and a small pulmonate *Onchidella patelloides.* Far outnumbering any of these, and in fact more numerous than the mussels themselves, is the tiny pelecypod *Lasaea australis. Lasaea* occurs in this and lower levels of the shore wherever there is sufficient shelter, among the *Galeolaria* tubes or among the close-growing algae such as *Corallina,* and it occurs similarly in New South Wales.

These associates of mussels also occur among the *Galeolaria* tubes and probably degree of shelter is the controlling factor in their appearance at higher levels. They do not appear at this height when only barnacles are present with consequent lack of shelter. Attached to the mussel valves are numerous small dark limpets, *Notoacmea* (*Conacmea*) *alta,* and in spring the alga *Porphyra* may form a band near the centre of the mussel's vertical range. Where good beds of mussels occurred, considerable numbers of the thaid shell *Dicathais textiliosa* appeared to be preying on them.

While *Dicathais, Notoacmea, Lasaea* and the polyclad were found throughout the geographical range of *Brachyodontes* in Victoria, the following species were found with them only east of Cape Otway: the anemone *Actinia tenebrosa,* the cirripede *Ibla quadrivalvis,* and the small pulmonate *Onchidella patelloides.* The area from which they are missing is where the coldest summer temperatures occur, and this might inhibit breeding.

Where there was plenty of shelter, such as inshore in Bridgewater Bay or in Nelson Bay, or at the back of the rock platforms just to the east of Cape Otway, a marked band of the alga *Ilea fascia* occurred on the rocks just above the *Brachyodontes* or in the upper part of its range.

Scattered on the rocks, between the upper clumps of *Brachyodontes* are a series of siphonarias, limpets, and in sheltered places, periwinkles which are found also among the clusters of *Chamaesipho* or between the specimens of *Chthamalus,* where the ranges of these two barnacles overlap. The commonest siphonaria is *S. diemenensis,* which has a fairly wide vertical range in the barnacle zone and is found all along the Victorian coast. It is also recorded in Tasmania on the exposed coasts (May 1923). *Ellsiphon scabra* (Reeve) has been recorded (Dakin, Bennett, and Pope 1948) on the open coast of New South Wales in the corresponding zone to that of *S. diemenensis* in the south. It is now considered that this northern species should have been called *S. denticulata* Q. & G.

Immediately above the level of the *Brachyodontes,* a bluish coloured siphonaria, *S. tasmanica,* covers a narrow vertical range. This species occurs along most of the Victorian coast, but in places a second species, *S. funiculata,* is also found in the upper littoral, and the present authors have collected it on the open coast to the east but not to the west of Cape Otway.

Among the true limpets which, together with siphonarias, mussels, and barnacles, form a mosaic pattern in the upper barnacle zone, are the following: *Notoacmea mayi, N. petterdi, Chiazacmea mixta, Patelloida nigrosulcata,* and *P. latistrigata.* Of these, *N. petterdi* was not collected west of Cape Otway. *P. nigrosulcata* was collected at Cape Nelson only. *N. mayi* was found along the western portion of the Victorian coast and was not found east of Phillip I., but it occurs on Tasmanian shores, according to the literature, and in collections examined by the authors. Oliver (1926) not only gives systematic descriptions of all these patelloid species but also supplies much data as to their geographical distributions.

In the upper part of the barnacle zone, there is a small predatory thaid, *Lepsiella vinosa,* which seems to play the same ecological role as *Morula marginalba* on the coast of New South Wales. On reasonably sheltered shores, several species of small gastropods occur in the upper half of the barnacle zone. They are *Austrocochlea obtusa, A. constricta, Bembicium melanostoma,* and juveniles of two littorinids, *Melaraphe praetermissa* and *M. unifasciata.* The adult *Melaraphe* generally occur in the supra-littoral.

A second band of mussels, *Modiolus pulex,* sometimes also appears in the upper part of the vertical range of the barnacle *Chamaesipho.* The position of this upper band, relative to the lower band of mussels (*Brachyodontes*), can be seen in Figure 4 in columns I, II, and III. Although the dark colour of *Modiolus* makes this band conspicuous, it rarely covers as wide an area as *Brachyodontes* because of its much narrower vertical range. *M. pulex* sometimes occurs in sheets on flattish rocks in the higher part of the littoral—even places where sand seems almost to bury the mussels, and it is possible to remove sheets of the sand and mussels packed together from the rocks. *Modiolus* occurred thus at Bridgewater Bay but in a number of other localities it grew attached to rocks in the high littoral, well beyond the influence of sand. It would seem from this that the association with sand was fortuitous.

Barnacles were abundant only at Wilson's Promontory and Hayley's Reef on the Victorian coast and for the most part there are fewer of any one barnacle species per unit area of the rocks than in equivalent areas in New South Wales. Thus west of Cape Otway, several counts revealed only 50 *Chamaesipho* barnacles per square foot (as against 3,000 at least in New South Wales), and as has already been stated, *Chthamalus antennatus* was absent altogether between Cape Otway and Cape Bridgewater, but is reported in South Australia at Robe. Both *Chamaesipho* and *Chthamalus* occur sparsely at Robe (S. Edmonds, personal communication).

Chthamalus antennatus lives near the upper margin of the littoral zone where it grades into the supra-littoral area of the shore, and is only covered during high spring tides.

(*c*) *The* Galeolaria *or Mixed Algal Turf Zone.*—Where wave action is submaximal, the next part of the littoral is covered by the closely packed tubes of the serpulid *Galeolaria caespitosa.* This band lies mainly in the lowest part of the shore area which Stephenson and Stephenson (1949) designated as "Balanoid Zone". The conditions which apparently favour or prevent the proper growth of this serpulid in New South Wales have already been described (Dakin, Bennett, and Pope 1948, pp. 213 et seq.). In Victoria it is believed that the same factors are operative.

The Galeolaria *association.*—Where the growths were thick enough to form cauliflower-like masses and not just a thin coating on the rocks, as seen in Plate 2, Figure 1, the spaces between the tubes are thickly populated by a cryptofauna which includes many errant polychaetes (*Perinereis novaehollandiae, Neanthes* sp., and several others not yet identified), gephyreans (*Phascolosoma japonica* and *Phascolosoma* sp.), a polyclad (closely allied to *Leptoplana*), which is common along with nemerteans, amphipods, tanaid crustaceans, small black limpets (*Notoacmaea* (*Conacmea*) *alta*), the little pelecypod (*Lasaea australis*), the slit limpets (*Montfortula conoidea* in eastern Victoria, or *M. rugosa* west of Cape Otway, and the small chiton (*Meturoplax retrojecta*).

These various species are uniformly present along the Victorian coast but east of Cape Otway three additional species, two of which are mentioned in the *Brachyodontes* association, are very common in this habitat. They are the stalked barnacle *Ibla quadrivalvis*, the spider *Desis crosslandi*, and the pulmonate *Onchidella patelloides*. West of Cape Otway these three species were absent and were not found between this Cape and Portland (approximately 200 miles of coast). According to Mr. S. Edmonds (personal communication) the first two reappear in the *Galeolaria* growths in South Australia.

The vertical width of the *Galeolaria* zone ranges from about 9 to 25 in., depending on the tidal range, being narrower in western Victoria and widest at Norman Bay, Wilson's Promontory (Plate 2, Fig. 1). The upper limit of the thick growth of *Galeolaria* terminates just as sharply in Victoria in the regions of constant high seas as in New South Wales. Also, as in New South Wales, individuals are found on shore levels both above and below the *Galeolaria* zone proper, for example in shallow depressions where water lies in the higher littoral, or on the tests of the ascidian, *Pyura*, below this zone. Only in the zone of the thick growths are their associates to be found.

In places too exposed for development of a thick *Galeolaria* growth, the rocks are covered by a weed mat in which coralline algae are dominant. In their shelter are numerous polychaete worms, amphipods such as *Hyale rupicola* and *Podoceros* sp., and some kelp shells. Limpets such as *Cellana tramoserica* or *Patellanax squamifera* also live on the rocks between the clumps of algae.

The commoner species found in the algal turf are:

Gymnosorus variegatus, Jania fastigiata, Padina frazeri, Pterocladia capillacea, Peyssonnelia gunniana, Caulerpa simpliciuscula, C. brownii, C. Corallina cuvieri, C. officinalis, Platysiphonia sp., *Laurencia heteroclada*, and stunted *Laurencia* spp. The upper boundary of this zone, whether covered by algae or by *Galeolaria*, is generally sharply demarcated.

(*d*) *The* Poneroplax *or "Bare" Zone.*—The population of the zone immediately below the *Galeolaria* varies according to the degree of exposure to wave action, and also as to whether it lies to the east or west of Cape Otway. All along the coast, however, it is marked by the presence of large chitons of the genus *Poneroplax*, which reach a length of 5 in. In New South Wales this region is usually completely covered by the ascidian *Pyura stolonifera* and this species occurs sporadically at a few places along the Victorian coast east of Cape Otway, e.g. Wilson's Promontory, Walkerville (only a few, scattered specimens), Lorne, and Apollo Bay. The ascidian occurs much as it does in the eastern State (Plate 1, Fig. 2; Plate 2, Fig. 1; Plate 4, Fig. 2). At Apollo Bay, the extreme western limit of its range on the open coast in Victoria, it is still quite plentiful and shows no sign of "thinning out". At Cape Otway, however, an efficient barrier seems to occur to prevent its spread westward.

Apart from those few localities where *Pyura* occurs, this zone on the shore appears bare because the species present are either few and scattered or are inconspicuous and low-growing like the "lithothamnion" which in most places coats the rocks. The chitons *Poneroplax costata* or *P. albida* mark this zone and a few scattered limpets such as *Patellanax squamifera* and *Cellana tramoserica* occur here, the latter appearing in Victoria at a lower level of the shore than it frequents in New South Wales. Sometimes, west of Cape Otway, the rocks in this zone are coated with a dark-coloured algal "scum" instead of by "lithothamnion". Dangerous seas and the smoothness of the rocks prevented the authors' obtaining samples for identification.

The Pyura *association.*—In the few localities where good growths of *Pyura* occurred, a number of associates were found. Here the thaid shell *Dicathais textiliosa* occurred in numbers, also the limpets *Patellanax squamifera* and *Patelloida alticostata*, and the turban shell *Subninella undulata*. The fissurellid *Montfortula conoidea* and small specimens of *Poneroplax* are two molluscs common in this situation, along with grey-coloured compound ascidians, small crustaceans such as tanaids and amphipods, polychaete worms, and an occasional seastar, *Patiriella calcar*. The upper limit of the *Pyura* band is rarely pushed up the shore except where the heaviest and most prevalent surge occurs.

In the *Poneroplax* zone, or its corresponding level, several species of the algal genus *Cystophora* occur. At Wilson's Promontory *C. intermedia* grew in exposed places among the *Pyura* or on nearly vertical rocks it even replaced the *Sarcophycus* completely down to low-water mark, occurring as described by Womersley (1948) at Kangaroo I., South Australia. On more sheltered coasts from Norman Bay to Cape Otway, *Cystophora torulosa* is found in this zone. Other species of *Cystophora* which occur are *C. paniculata*, *C. uvifera*, *C. retorta*, or *C. siliquosa*, and these are usually found where the shore is somewhat sheltered or in rock pools in this part of the littoral (Plate 6, Fig. 2).

In some localities *Balanus nigrescens* occurred as a definite fringe at the upper border of this zone but elsewhere it was sparser. This fringe was only a few inches in vertical height and in it the barnacle exhibited its tall growth form (approximately 1½-2 in. high and tubulo-conical in shape). This species may also live at a slightly lower level among the *Pyura* tests, but there it is usually smaller and has a different shape. It favours exposed places for it is reduced or absent on more sheltered rocks and is replaced largely by the alga *Hormosira banksii*.

Hormosira has only a narrow vertical range in Victoria, as in New South Wales, but where a large, fairly level rock platform occurs within this narrow vertical range, the *Hormosira* carpets a wide area. Where such a wide expanse of *Hormosira* occurs, as at Walkerville, Waratah Bay, or in places near Lorne, the epiphytic alga *Cladostephus verticillatus* grows on it, and there may also be associated with it a number of species of *Codium* and *Caulerpa* and the coralline *Jania micrarthrodia.* Because the presence of *Hormosira* is indicative of a certain degree of shelter, the numbers of molluscs, echinoderms, worms, crustacea, sponges, coelenerates, etc. found there are very much higher than on more exposed rocks and one can scarcely apply the term "bare" to it.

The following list of animals taken in this area at Walkerville indicates the richness of the fauna occupying this part of the shore in a sheltered locality:

MOLLUSCA
  Chitons: *Ischnochiton clongatus, I. milligani, Ischnoradsia australis, Heterozona subviridus, H. fruticosa*
  Gastropoda: *Haliotis ruber, Scutus antipodes, Ambiychilepas javanicensis, Montfortula conoidea, Austrocochlea odontis, Micrastraea aurea, Subninella undulata, Cymatilesta spengleri, Dicathais textiliosa, Cominella lineolata, Patelloida alticostata*
  Pelecypoda: *Lasaea australis, Vulsella spongiarum* (in sponge)

ECHINODERMATA
  Asteroidea: *Coscinasterias calumaria, Patiriella calcar, P. exigua, P. brevispina, Nectria ocellata, Tosia australis, Allostichaster polyplax*
  Echinoidea: *Holopneustes* (intermediate between *H. pycnotilus* and *H. inflatus*), *H. porosissimus, H. inflatus, Amblypneustes ovum* var. *pachistus*
  Ophiuroidea: *Placophiothrix spongicola, Ophionereis schayeri*
  Holothuroidea: *Mensamaria thomsoni*
  Crinoidea: spp. unidentified

CRUSTACEA
  Amphipoda: *Hyale* sp.
  Anomura: *Axianassa* sp., *Lomis hirta*
  Cirripedia: *Elminius simplex*
  Brachyura: *Pilumnus tomentosus, Halicarcinus ovatus, Paramithrax latrielli*
  Caridea: *Palaemon* (olim *Leander*) *serenus*

POLYCHAETA
  Errantia: Polynoid (not identified), nereid worms among algae

TUNICATA
  Compound ascidians (unidentified)
  Pyura sp. (stalked)

COELENTERATA
  Actiniaria: *Actinia tenebrosa, Oulactis muscosa, Cnidopus verater*
  Hydroida: Many spp. hydroids on weeds

BRYOZOA
  Cryptopolyzöon sp.
  Red, or orange-red, encrusting weeds

PORIFERA
  Tethya corticata, Scypha sp. Spp. unidentified

This list is not exhaustive.

This vertically narrow fringe to the *Poneroplax*-Bare zone has an abruptly defined upper limit and passes without gradation into the *Galeolaria* or mixed algal turf.

(*e*) *The Zone of the Large Brown Algae.*—Immediately below the *Poneroplax*-bare zone lies the area characteristically marked by the large "bull kelp", *Sarcophycus potatorum* (Plate 1, Fig. 2; Plate 5). This zone is exposed only by low spring tides during calm weather (Plate 1, Fig. 2). During normal sea conditions, at low water, the upper plants in the *Sarcophycus* band are awash. Despite this constant surge, there is generally a clearly defined upper limit to this zone. Only in places with absolutely maximal exposure (e.g. on the tip of one or two points at Cape Bridgewater, near Portland) was the upper limit of the *Sarcophycus* zone pushed up the shore. Plate 5, Figure 2, shows one such point with the *Sarcophycus* growing up to a higher level because of continuous heavy swells on the seaward aspect of a jutting point of rock. The waves caused by a ground swell were the largest encountered during normal conditions at any point along the 2000 miles of coast surveyed by the authors.

While *Sarcophycus* is almost universally present on the exposed coast of Victoria, a few additional brown algae are also found in this lowest shore zone under suitable conditions. For instance, *Cystophora intermedia* replaced *Sarcophycus* in one or two limited areas of rock on the eastern shore of Wilson's Promontory where the rocks were nearly vertical. This species was not observed, however, at any other Victorian locality but it has been recorded further west in South Australia in a similar situation (Womersley 1947, 1948). Certain localities at Phillip Island apparently offer similar conditions to those at Wilson's Promontory but no *C. intermedia* was seen.

At Bastion Point, near Mallacoota Inlet, in Waratah Bay, and at Sorrento, the tops of the fronds of another very large brown alga, the kelp *Macrocystis integrifolia*, are exposed at low water. *Macrocystis* grows slightly lower down than *Sarcophycus*, and in places which are slightly sheltered. It is often cast up but is only accessible in very large and deep rock pools in the lowest part of the littoral, or in the deep troughs between stacks and reefs, as at Bastion Point.

Two further large brown algae, *Ecklonia radiata* and *Phyllospora comosa*, occur also in the lowest part of the intertidal zone—generally in sheltered places or deep rock pools. Whereas in New South Wales these two species are the dominants in the kelp zone (together with corallines such as *Arthrocardia, Corallina, Lithothamnion*,* and *Amphiroa anceps*, which form an undergrowth), in Victoria they play a secondary role to *Sarcophycus* and are absent in very exposed places.

Sarcophycus fringes the shores of the mainland of the continent between Bermagui, N.S.W., and Robe, S.A., and is also recorded round the Tasmanian coast.

Between the plate-like holdfasts of *Sarcophycus*, the rocks are coated with "lithothamnion". One species of limpet, *Patellanax squamifera*, commonly inhabits the rocks of this zone, its shells generally being coated with "lithothamnion". An occasional large chiton (*Poneroplax*) is also found among the large holdfasts. Careful examination of the fronds and holdfasts of the *Sarcophycus* further revealed only one isopod, *Amphoroidea australiensis*, clinging to the alga and no other animals or epiphytic growths.

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* "Lithothamnion" spp. unidentified.

(ii) *General Remarks on Victorian Zonation*

Colman (1933), Fischer-Piette (1936), W. Stephenson (1941), Chapman (1943), Evans (1947), Beveridge and Chapman (1950), and Dellow (1950) have correlated the vertical ranges of intertidal marine organisms with tidal levels and percentage exposure to air. They have found a number of critical levels on the shore which determine the boundaries (either upper or lower) to the vertical ranges of certain of the intertidal organisms. These critical levels evidently mark certain heights above low-water mark where the environment changes so markedly in some important factor or factors that some species cannot live above it and others cannot live below it. The shore is thus divided into a number of clearly defined, horizontal zones, each supporting its own association of animals.

It was Doty (1946) who first showed most convincingly the connexion between tidal factors which produced certain critical levels and thus limited the vertical ranges of the series of zones in the intertidal area. At these critical (tide) levels, owing to the irregularities and variations of the tides, sudden two- or threefold increases occurred in the amount of exposure to changes in the environment. These changes are sufficiently marked to account for the clear-cut margins of some of the vertical ranges of plants and animals. It is believed that critical tide levels will be found in Victoria to occur at the heights above low-water level which mark the upper limits of the following zones: (1) *Sarcophycus potatorum*, (2) *Pyura stolonifera*, (3) *Galeolaria caespitosa*, and (4) *Brachyodontes rostratus*. Other critical levels will, no doubt, also be determined, but the four mentioned seem obvious from inspection.

The pattern of intertidal zonation in Victoria differs significantly from that of New South Wales as follows:

(1) In the supra-littoral, a different species of *Melaraphe*, *M. praetermissa*, makes its appearance in addition to *M. unifasciata*, while *Nodilittorina tuberculata* is absent, except on the far east coast. It was absent at Wilson's Promontory and only a very few scattered individuals were found at Bastion Point, Mallacoota. The presence of the isopod *Ligia australiensis* on the open coast is characteristic of the western part of Victoria and (see Edmonds 1948) of eastern South Australia.

Although it might appear from Figure 4 that the dark band of lichens occurred only in the more westerly part of the State, this is not so for it is a prominent feature in the east at Waratah Bay, just to the west of Wilson's Promontory, and it is present at Bastion Point, Mallacoota, although not as a dominant organism and so not shown in Figure 4, column IV.

(2) In the littoral, the presence of two bands of mussels, *Modiolus pulex* and *Brachyodontes rostratus,* is in marked contrast to conditions in New South Wales. With one or two exceptions, the numbers of each species of barnacle in this zone are reduced when compared with those of the central New South Wales coast, but the numbers, both of species and of individuals, of small limpets is increased. The barnacle *Tetraclita rosea* is absent in Victoria (except on the extreme east coast—only two or three scattered individuals were seen at Bastion Point). Two bands of algae are also characteristic of the colder region, *Ilea fascia* and *Splachnidium rugosum.* The latter occurs in New South Wales as a band only in the far south, e.g. at Green Cape.

(3) The ascidian *Pyura stolonifera* is not general in its occurrence in Victoria, and is more often absent than present. It just happens to be found in three of the particular localities chosen for illustration in Figure 4, and occurs but rarely elsewhere. This part of the shore is more characteristically "bare" or covered by growths of *Cystophora* spp. The average size of the *Poneroplax* in this zone is much larger in Victoria than in New South Wales.

(4) The large brown algae of the infra-littoral fringe in Victoria are different from those in both New South Wales and South Australia, though the species from New South Wales may occur in sheltered situations in Victoria (e.g. rock pools).

A number of species both of plants and animals are common to the two areas and some of them occur similarly and may be equally abundant in both places, e.g. *Galeolaria.* Others flourish better in the warmer waters of New South Wales and yet others in the cooler Victorian waters. A species may thus be found in both areas and yet show a difference in occurrence. For example, the barnacle *Chamaesipho columna* is as much as two or three times taller in Victoria than in New South Wales. The alga *Hormosira banksii* not only flourishes better in the south but also grows lower on the shore (below the *Galeolaria* in Victoria and above it in most of New South Wales). Also the two species of *Cystophora* which occur both in the warmer and colder waters flourish best in the south. Further examples will be cited in the biogeographical section of this paper.

The change from what may be termed the typical zonation pattern of the warm-temperate coasts of New South Wales to that of the cool-temperate one of Victoria takes place gradually rather than suddenly, and there is a long stretch of coast where overlapping occurs. As might be expected, the more easterly section of the Victorian coast shows affinity in its zonation with that in New South Wales. Further westward the resemblance becomes less marked, as one prominent species or another drops out until, west of Cape Otway, the dominant shore forms are markedly different. From here west they begin to show affinities with the dominants described at Kangaroo I. in South Australia (Edmonds 1948; Womersley 1947, 1948). There may thus be a considerable overlap between the western, warm-temperate zonation of the Flindersian Province of Cotton (1930), and the Victorian one.

To assist other workers to estimate this overlap Table 2 lists the commoner organisms on the Victorian coast. This list will serve as a census of the species that are ecologically prominent in the new cool-temperate province proposed below (Section III).

(iii) *Common Animals and Plants of the Intertidal Zone of the Exposed Rocky Coast of Victoria*

Many species of worms, hydroids, and small crustaceans have not been identified and are excluded from Table 2. For the purpose of recording the approximate geographical ranges of species in this list the coast has been divided into three sections. The eastern one stretches from Mallacoota to Phillip I., the central section from Sorrento to Apollo Bay, and the western section from Cape Otway to Cape Bridgewater. An "x" in any one locality column signifies that the species was collected by the present authors; a "—" indicates that it was absent or not collected. The relative abundance of any species will be indicated by the following: x = present, xx = numerous, and xxx = very plentiful. The vertical ranges will be roughly indicated by using the symbols (*a*), (*b*), (*c*), (*d*), (*e*) to show in which of the five basic zones, as defined in Section II (*B*) (i) (Fig. 2) the species occur.

Representative specimens of all mollusc species collected are housed in the National Museum of Victoria.

TABLE 2

LIST OF COMMON ORGANISMS

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
ANIMALS					
PORIFERA					
Scypha sp. (olim Sycon)	x	x	—	(*d*), (*e*)	Lowest part of the littoral and infra-littoral fringe
Tethya corticata Lend.	x	x	—	(*d*), (*e*)	"
Six additional species undetermined					"
COELENTERATA					
HYDROIDA					
Obelia australis von Lend.	x	—	—	(*e*)	Attached to algae
Sertularia operculata Linn.	—	—	x	(*e*)	"
Hydroida spp. undet.	x	x	x	(*e*)	

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
ACTINIARIA					
Actinia tenebrosa Farq.	xx	xx	xx	(*b*), (*c*)	
Anthothoë albocincta (Hutt.)	x	x	x	(*e*)	
Oulactis muscosa (Dray.)	x	x	x	(*b*), (*c*)	
Cnidopus verater (Dray.)	x	x	x	(*b*), (*c*)	
Brown anemones	—	—	xx		Fairly common
Sand-burrowing anemones	x	—	—	(*e*)	
CORALLIMORPHARIA					
Corynactis australis Hadd. and Duerd.	x	—	—	(*e*)	Recorded at Julia Percy I. by McCoy Society (1937)
VERMES					
TURBELLARIA					
Leptoplana ? australis Laidlaw	xx	xx	—	(*b*), (*c*)	Among *Galeolaria* tubes
Turbellarian (with yellow ground colour and orange border)	x	—	—	(*d*)	
NEMERTINEA					
Nemertean spp.					
1. Among *Galeolaria*	xx	xx	xx	(*c*)	
2. „ *Brachyodontes*	xx	xx	xx	(*b*)	
3. „ seaweed mat	x	x	x	(*c*), (*d*)	
ANNELIDA					
POLYCHAETA					
Lepidonotus bowerbankii Baird	?x	x	—	(*d*)	
Nereid worms in					
1. *Pyura*	xx	xx	—	(*d*)	
2. *Galeolaria*	xx	xx	xx	(*c*)	
3. *Brachyodontes*	x	x	x	(*b*)	
Perinereis novaehollandiae Kinberg	xx	xx	xx	(*b*), (*d*)	
Glycera sp.	—	x	x	(*d*), (*e*)	
Eunice sp. large	x	x	x	(*d*)	
Diopatra dentata Kinb.	x	—	—	(*e*)	Virtually absent in Victoria — only one specimen seen
Cirratulus sp.	x	—	—	(*d*)	
Arenicola sp.	—	—	x	(*e*)	Burrowing in sand
Maldanid sp.	—	x	—	(*e*)	” ” ”
Idanthyrsus pennatus (Peters)	x	x	—	(*d*)	
Sabella sp.	x	—	—	(*d*)	
Sabellastarte indica Sav.	—	x	—	(*d*)	In deep pools
Spirorbis sp. or spp.	x	x	x	(*c*), (*e*)	
Serpula sp.	x	—	x	(*c*), (*d*)	
Galeolaria caespitosa Lam.	xx	xx	xx	(*b*), (*d*)	

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
G. hystrix Mörch.	x	—	—	(*d*)	
Salmacina dysteri Huxley	x	x	x	(*d*)	
GEPHYREA					
Phascolosoma spp.	xx	xx	xx	(*b*), (*d*)	(Genus as defined in 1952 by W. K. Fisher)
BRYOZOA					
Scrupocellaria ? scrupea Busk	—	x	—	(*e*)	
Menipea crystallina Gray	—	x	—	(*d*)	
Retepora fissa Gray	—	x	—	(*d*)	
Discopora ellerii MacGill.	—	x	—	(*d*)	
Scuticella margaritacea Busk	—	x	—	(*d*)	
Holoporella sp.	x	xx	—	(*d*)	
Villaticella ? elegans Busk	x	xx	—	(*d*)	
Membranipora membranacea Linn.	—	x	—	(*d*)	
Cryptopolyzoon sp.	x	x	x	(*d*)	
BRACHIOPODA					
Terebratulid	—	x	—	(*d*)	Specimens not identified
MOLLUSCA					
LORICATA					
Poneroplax costata (Blainv.)	x	xx	xx	(*d*), (*e*)	Not taken east of Walkerville
P. albida (Blainv.)	xx	xx	xx	(*d*), (*e*)	
Ischnochiton elongatus elongatus (Reeve)	x	x	—	(*d*)	
I. versicolor (Sowerb.) *milligani* Ired. & May	xx	x	—	(*d*)	Recorded only as far north as Eden, N.S.W.
I. lineolatus (Blainv.)	—	x	—	(*d*)	
Ischnoradsia australis (Sowerb.)	x	x	—	(*d*)	Recorded in S. Aust. also
Haploplax smaragdina (Angas)	x	—	—	(*c*), (*d*)	Common but only taken at Walkerville
Meturoplax retrojecta Pilsbry	xx	xx	xx	(*c*), (*d*)	Associated with *Pyura* and *Galeolaria*
Heterozona fruticosa (Gould)	x	—	—	(*d*)	
H. cariosa Dall.	—	x	x	(*d*)	
H. subviridis Ired. & May	xx	x	—	(*d*), (*e*)	
GASTROPODA					
Fam. Fissurellidae					
Scutus antipodes Montfort	x	x	—	(*d*), (*e*)	Recorded at Julia Percy I.
Montfortula conoidea (Reeve)	xx	xx	x	(*c*), (*d*)	Includes *M. rugosa*

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Amblychilepas javanicensis (Lam.)	—	xx	—	(*c*), (*d*)	
Sophismalepas nigrita (Sow.)	x	x	—	(*c*), (*d*)	
Fam. Haliotidae					
Haliotis ruber (Leach)	x	x	x	(*d*), (*e*)	
Fam. Trochidae					
Austrocochlea odontis (Wood)	x	x	—	(*d*)	
A. constricta obtusa (Dillw.)	x	—	—	(*b*), (*c*)	
A. constricta constricta (Lam.)	xx	xx	x	(*b*), (*c*)	
A. adelaidae (Philippi)	x	xx	xx	(*c*), (*d*)	
A. concamerata (Wood)	x	x	x	(*b*), (*c*)	
Clanculus plebejus (Philippi)	xx	xx	x	(*c*), (*d*)	
Cantharidus ramburi (Crosse)	—	x	—	(*c*), (*d*)	
Clanculus undulatus (Lam.)	—	—	x	(*c*), (*d*)	
Herpetopoma aspersa (Philippi)	x	—	—	(*d*)	Called *Euchelus baccatus* in 1948 work
Fam. Stomatellidae					
Stomatella imbricata Lam.	x	—	—	(*d*)	At Walkerville only
Fam. Turbinidae					
Micrastraea aurea (Jonas)	x	x	?x	(*d*)	
Subninella undulata (olim Turbo) (Solander)	xxx	xxx	xxx	(*c*)to(*e*)	Larger than in New South Wales
Fam. Neritidae					
Melanerita melanotragus (Smith)	xx	xx	xx	(*a*)to(*c*)	
Fam. Patellidae					
Cellana tramoserica (Sower.)	xx	xx	xx	(*b*)to(*d*)	
Patellanax squamifera (Reeve)	xx	xx	xx	(*c*)to(*e*)	Includes species called *P. peronii* (Blainv.)
Fam. Acmaeidae					
Patelloida alticostata (Angas)	xx	xx	xx	(*c*)to(*e*)	
P. latistrigata (Angas)	x	x	x	(*a*), (*b*)	Equivalent of *P. submarmorata* of New South Wales
P. submarmorata (Pilsbry)	xx	—	—	(*a*), (*b*)	At Mallacoota only
P. nigrosulcata (Reeve)	—	—	x	(*b*)	At Cape Nelson only
Notoacmea mayi (May)	—	xx	xx	(*a*), (*b*)	West of Phillip I. only
N. petterdi (Ten.-Woods)	x	x	—	(*a*), (*b*)	From Cape Otway east
N. scabrilirata (Angas)	x	x	x	(*b*), (*c*)	Under stones below mid-tide level
N. septiformis Q. & G.	—	—	x	(*b*)	Cape Nelson only
Chiazacmea mixta (Reeve)	xx	xx	xx	(*a*)to(*c*)	Includes several subspecies
Conacmea alta Oliver	xx	xx	xx	(*b*), (*c*)	On shells of *Brachyodontes*

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Fam. Littorinidae					
Melaraphe unifasciata (Gray)	xx	xx	xx	(*a*), (*b*)	
M. praetermissa (May)	x	xx	xx	(*a*), (*b*)	Favoured by shelter
Fam. Bembiciidae					
Bembicium melanostoma (Gmelin)	xx	xx	xx	(*b*)	Includes *B. nanum*
Nodilittorina tuberculata (Menke)	x	—	—	(*a*)	Taken only at Mallacoota
Fam. Vermetidae					
Vermetid sp.	x	—	—	(*d*)	
Fam. Capulidae					
Capulus australis Lam.	x	—	x	(*c*), (*d*)	On shells of *Subninella*
Fam. Cymatiidae					
Cymatilesta spengleri (Perry)	x	x	—	(*d*), (*e*)	
Fam. Cypraeidae					
Notocyprea angustata (Gmelin)	x	—	x	—	Dead shells only
Fam. Conidae					
Floraconus anemone (Lam.)	x	x	x	(*d*)	
Fam. Fasciolariidae					
Fasciolaria australasia (Perry)	x	x	—	(*d*)	
Fam. Buccinidae					
Cominella lineolata (Lam.)	xx	xx	xx	(*c*), (*d*)	Also found in southern New South Wales
Fam. Thaiidae					
Dicathais textiliosa (Lam.)	xx	xx	xx	(*b*) to (*e*)	See page 145
Lepsiella vinosa (Lam.)	x	xx	xx	(*a*), (*b*)	Seems to replace *Morula marginalba* of New South Wales
Fam. Muricidae					
Agnewia tritoniformis (Blainv.)	x	—	—	(*c*), (*d*)	
Fam. Siphonariidae					
Siphonaria (*Ductosiphonaria*) *diemenensis* Q. & G.	xx	xx	xx	(*b*)	For this nomenclature see Hubendick (1946)
Siphonaria (*Pachysiphonaria*) *tasmanica* Ten.-Woods	—	xx	xx	(*b*)	„
Siphonaria (*Pachysiphonaria*) *funiculata* Reeve	x	x	—	(*b*)	„
Fam. Onchidiidae					
Onchidella patelloides (Q. & G.)	xx	xx	—	(*c*), (*d*) (*d*)	Among *Brachyodontes* shells and *Galeolaria* tubes and on rocks in lowest littoral

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Fam. Dorididae					
Dendrodoris carneola (Angus)	—	x	—	(*d*)	
Fam. Pleurobranchaeidae					
Pleurobranchus sp.	—	—	x	(*d*)	
PELECYPODA					
Fam. Arcidae					
Arca pistachia Lam.	—	x	—	(*d*)	
Fam. Vulsellidae					
Vulsella spongiarum Lam.	x	—	—	(*e*)	
Fam. Mytilidae					
Mytilus planulatus Lam.	x	—	x	(*b*)to(*d*)	In sheltered spots
Modiolus pulex Lam.	x	xx	xx	(*b*)	Often with admixed sand
Brachyodontes rostratus (Dunk.)	xx	xxx	x	(*b*)	See note page 150
B. erosus (Lam.)	—	x	—	(*b*)	See note page 150
Fam. Laternulidae					
Laternula sp. (dead shells)	x	—	—	(*d*)	
Fam. Erycinidae					
Lasaea australis Lam.	xxx	xxx	xx	(*b*)to(*d*)	Larger size than in New South Wales
Fam. Veneridae					
Venerupis crenata Lam.	x	—	—	(*d*)	
Fam. Hiatellidae					
Hiatella australis (Lam.)	—	x	x	(*d*)	Portland pier (for western spec.)
CEPHALOPODA					
Amplisepia apama (Gray)	x	—	x	—	Dead shells only
Octopus cyaneus Gray	—	—	—	—	Said to occur in Victoria
ARTHROPODA					
CRUSTACEA					
DECAPODA					
Caridea					
Palaemon serenus (Heller)	x	x	—	(*d*)	olim Genus *Leander*
Leptochela—like prawn	—	—	x	—	Cast shells only
Betaeus sp.	—	—	x	—	„ „ „
Anomura					
Lomis hirta (M. Edw.)	xx	xx	—	(*d*)	Among boulders
Callianassa ceramica Fult. & Grant	—	x	—	(*d*)	„ „ in sand
Upogebia sp.	—	x	—	(*d*)	
Axianassa sp.	x	x	—	(*d*)	
Brachyura					
Plagusia capensis (Linn.)	x	x	x	(*d*)	
Paramithrax latrielli Miers	x	x	—	(*d*)	

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Paragrapsus quadridentatus (M. Edw.)	x	x	x	(*a*), (*b*)	Seems to replace *Leptograpsus variegatus* of New South Wales
Cyclograpsus audouinii (M. Edw.)	x	x	x	(*a*), (*b*)	
Halicarcinus ovatus (Stimp.)	x	x	—	(*c*), (*d*)	
Pilumnus tomentosus (Latr.)	x	x	—	(*d*)	
Nectocarcinus integrifrons (Latr.)	x	x	—	(*d*)	
Brachynotus octodentatus (M. Edw.)	—	x	x	(*a*)	
Naxia tumida (Dana)	x	—	—	(*c*), (*d*)	
Mictyris platycheles M. Edw.	x	x	—	—	On sandy beaches only
Ovalipes bipustulata M. Edw.	—	—	x	(*e*)	” ” ” ”
Carcinides moenas (Pennant)	x	—	—	(*b*)	Introduced (Fulton and Grant 1900)
Cirripedia					
Ibla quadrivalvis Cuv.	xx	xx	—	(*b*), (*c*)	Larger than in New South Wales
Chthamalus antennatus Darw.	x	x	—	(*a*), (*b*)	
Chamaesipho columna (Spengler)	xxx	xx	x	(*b*)	
Catophragmus polymerus Darw.	xx	xx	x	(*b*)	
Balanus nigrescens Lam.	x	x	x	(*d*)	Sparse
Eliminius simplex Darw.	x	x	—	(*d*)	
Tetraclita purpurascens (Wood)	xx	xx	xx	(*b*), (*c*)	In places sheltered from sun, i.e. sides of gutters and boulders
T. rosea (Krauss)	—	x	—	(*b*)	Only in extreme east (Mallacoota), single specimens. Absent from Wilson's Promontory
Tanaidacea					
? *Euidotea* sp.	—	—	xx	(*d*)	
Isopoda					
Ligia australiensis (Dana)	—	xx	xxx	(*a*)	On high shore under stones by day
Cymodoce ? gaimardii (M. Edw.)	x	—	—	(*a*)	
Amphipoda					
Hyale rupicola (Hasw.)	—	x	x	(*c*), (*d*)	On algae
Hyale sp. nov. fide Sheard	x	—	—	(*c*), (*d*)	
Podoceros sp. near *laevis* Hasw.	—	—	x	(*c*), (*d*)	
Talorchestia ? diemenensis (Hasw.)	—	x	x	(*a*)	On high shore sand

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Arachnida					
Desis ? crosslandi Pocock	x	x	—	(*c*)	Among *Galeolaria* tubes
ECHINODERMATA					
ECHINOIDEA					
Holopneustes inflatus Ag.	x	—	—	(*d*), (*e*)	
H. intermediate between *inflatus* Ag. *pycnotilus* H.L.C.	x	—	—	(*d*), (*e*)	See page 151
H. porosissimus Sg. & Desor	xx	—	—	(*d*), (*e*)	
Amblypneustes ovum var. *pachistus* Clark	x	x	—	(*d*)	
Heliocidaris erythrogramma subsp. *hartmeyeri* Död.	x	x	—	Below (*e*)	Subtidal in sheltered places
ASTEROIDEA					
Austrofromia polypora (Clark)	x	x	—	(*d*)	
Patiriella exigua (Lam.)	xx	xx	xx	(*b*)	
P. calcar (Lam.)	xx	xx	—	(*b*), (*c*)	
P. brevispina H. L. Clark	xx	x	—	(*d*)	
Allostichaster polyplax (M. & T.)	x	x	—	(*d*)	
Tosia australis (Gray)	xx	xx	—	(*d*)	
Nectria ocellata Perrier	xx	x	—	(*d*)	Intertidal — dredged in New South Wales and Western Australia
Coscinasterias calamaria (Gray)	x	x	—	(*d*)	
CRINOIDEA					
Feather star (undetermined)	x	xx	—	(*d*), (*e*)	Under boulders
OPHIUROIDEA					
Ophionereis schayeri (M. & T.)	x	—	—	(*d*)	
Placophiothrix spongicola (Stimp.)	x	—	—	(*d*), (*e*)	
HOLOTHUROIDEA					
Mensamaria thomsoni (Hutton)	xx	xx	—	(*d*)	
Pentacta australis (Ludwig)	—	—	x	(*d*)	
ASCIDIACEA					
Pyura stolonifera (Heller)	x	xx	—	(*d*)	Only in certain localities. See text
P. australis (Q. & G.)	x	x	x	(*d*), (*e*)	
Botrylloides sp.	x	x	—	(*e*)	
Ciona intestinalis (Linné)	—	x	—	(*d*)	
Styela etheridgei Herd.	—	x	—	(*d*)	

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Sandy ascidian on *Cymodocea* plants	x	x	—	(*e*)	
Ascidians spp.					
PLANTS					
ALGAE					
CHLOROPHYCEAE					
Ulva lactuca Linn.	x	x	x	(*b*), (*c*)	
Enteromorpha intestinalis (L.) Link.	x	—	xx	(*a*)	
Bryopsis australis Sonder	—	—	x	(*d*)	
Cladophora sp.	x	x	x	(*b*) to (*d*)	
Caulerpa brownii Endl.	xx	x	xx	(*d*), (*e*)	Lowest part of littoral
C. cactoides (Turn.) Ag.	x	—	—	(*d*), (*e*)	" " " "
C. sedoides (R.Br.) Ag.	x	—	—	(*d*), (*e*)	" " " "
C. simpliciuscula (Turn.) Ag.	xx	—	xx	(*d*), (*e*)	" " " "
Codium pomoides J. Ag.	x	—	x	(*d*)	" " " "
C. lucasii Setchell	x	—	—	(*d*), (*e*)	" " " "
C. galeatum J. Ag.	x	x	—	(*d*)	" " " "
C. fragile (Suring) Hariot	x	x	x	(*d*)	" " " "
C. spongiosum Harv.	—	x	—	(*d*)	" " " "
PHAEOPHYCEAE					
Ectocarpus sp.	x	—	x	(*b*) to (*d*)	
Pocockiella (*Gymnosorus*) *variegatus* (Lam.) Papenfuss	xx	xx	—	(*c*), (*d*)	
Zonaria canaliculata J. Ag.	—	—	x	—	In beach wrack
Z. spiralis (J. Ag.) Papenfuss	—	—	x	—	"
Z. subarticulata (Lamour) Papenfuss	x	x	—	—	"
Rivularia atra Roth.	x	—	x	(*b*)	
R. australis Harv.	x	—	—	(*a*), (*b*)	
R. firma Wom.	x	—	—	(*b*)	
Scytothamnus australis Hook & Harv.	x	—	—	(*d*), (*e*)	
Cladostephus verticillatus (Lightf.) Ag.	x	x	—	(*d*)	Attached to *Hormosira* fronds
Padina frazeri (Grev.) J. Ag.	xx	xx	—	(*d*)	
Dictyopteris nigricans Wom.	—	—	x	—	In wrack
Corynophloea cystophorea J. Ag.	x	—	—	(*d*), (*e*)	Lower littoral and infra-littoral
Leathesia difformis (Linn.) Aresch	x	—	—	(*d*), (*e*)	"
Leathesia sp.	x	x	x	(*d*), (*e*)	
Colpomenia sinuosa (Roth.) Derb. & Sol.	x	x	x	(*c*), (*d*)	
Ecklonia radiata (Turn.) J. Ag.	x	x	x	(*e*)	Rare and in pools or wrack

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Macrocystis integrifolia (Linn.) Ag.	xx	x	x	Below (*e*)	
Splachnidium rugosum (Linn.) Grev.	xx	xx	x	(*b*)	Seasonal (warmer months)
Sarcophycus potatorum (Labill.) Keutz.	xxx	xxx	xxx	(*e*)	
Hormosira banksii (Turn.) Dec.	xx	xxx	xx	(*d*)	Grows at lower level in Victoria
Phyllospora comosa (Labill.) Ag.	xx	x	x	(*e*)	In pools and wrack
Cystophora uvifera (Ag.) J. Ag.	xx	x	—	(*d*), (*e*)	
C. torulosa (R. Br.) J. Ag.	xx	xx	—	(*e*)	On shores of Bass Strait
C. subfarcinata (Mert.) J. Ag.	xx	xx	x	(*d*), (*e*)	
C. cuspidata J. Ag.	—	x	x	(*d*)	
C. siliquosa J. Ag.	x	—	x	(*d*)	
C. intermedia J. Ag.	x	—	—	(*d*), (*e*)	On vertical rock faces
C. retorta (Mert.) J. Ag.	x	—	—	(*d*)	
C. spartioides (Turn.) J. Ag.	—	x	x	(*d*)	
C. platylobium (Mert.) J. Ag.	—	x	—	(*d*)	Lower littoral
C. polycystidae Aresch.	x	x	x	(*d*)	
C. paniculata (Turn.) J. Ag.	—	x	x	(*d*)	
C. dumosa (Grev.) J. Ag.	—	—	x	—	In wrack
Sargassum muriculatum J. Ag.	—	—	x	—	”
S. verruculosum (Mert.) J. Ag.	—	x	—	(*d*)	
S. bracteolosum J. Ag.	x	x	—	(*d*)	
S. halitrichum (Aresch.) J. Ag.	—	x	—	(*d*)	
Sargassum spp. stunted	x	x	x	(*d*)	
Ilea fascia (Muell.) Fries.	—	xx	xx	(*b*)	
RHODOPHYCEAE					
Gelidium pusillum (Stackh.) Le Jol.	x	x	x	(*b*)	
G. glandulaefolium Hook & Harv.	—	—	x	(*b*)	
Pterocladia capillacea (Gmel.) Born. & Thur.	x	x	x	(*d*), (*e*)	
Peyssonnelia gunniana J. Ag.	x	—	—	(*d*)	
Corallina officinalis Linn.	x	x	x	(*d*)	
C. cuvieri Lamour.	x	x	x	(*d*)	
Corallina spp. stunted	xx	xx	xx	(*d*)	
Jania micrarthrodia Lamour.	x	x	—	(*d*), (*e*)	
J. fastigiata Harv.	x	x	—	(*d*), (*e*)	
Lithothamnion sp. dark	x	x	x	(*d*), (*e*)	
Lithothamnion sp. light	x	x	x	(*d*), (*e*)	
Arthrocardia sp.	x	—	—	(*e*)	

TABLE 2 (*Continued*)

Name	Bastion Point, Mallacoota to Phillip I.	Sorrento to Apollo Bay	Cape Otway to Portland	In Vertical Zone	Remarks
Champia compressa Harv.	x	x	—	(*d*)	
Polysiphonia argus Kuetz.	—	—	x	(*b*)	
P. nigrita Sond.	—	—	x	—	Grows on *Perithalia inermis* (R. Br.) J. Ag.
P. frutex Harv.	—	—	x	(*d*)	Grows on *Hormosira banksii*
Dasyopsis clavigera Wom.	—	x	—	(*e*)	
Dasya naccaroides Harv.	—	x	—	(*e*)	Infra-littoral fringe
Melanthalia obtusata (Labill.) J. Ag.	—	x	—	(*e*)	"
Cheilosporum sagittatum (Lamour.) Aresch.	—	x	—	(*e*)	Infra-littoral fringe
C. sp.	x	—	—	(*e*)	"
Dicranema grevillei Sond.	—	x	—	(*e*)	"
Xiphophora chondrophylla (R. Br.) Mont.	x	—	—	(*e*)	"
Plocamium sp.	x	—	—	(*e*)	"
Ballia scoparia Harv.	x	—	—	(*e*)	"
Lophosiphonia sp.	x	—	—	(*d*)	
Laurencia filiformis (Ag.) Mont.	—	—	x	(*d*)	
L. elata (Ag.) Harv.	—	—	x	(*d*), (*e*)	
L. heteroclada Harv.	x	—	x	(*d*), (*e*)	
Laurencia stunted	x	x	xx	(*d*)	
Antithamnion sp.	—	x	—	—	In wrack
Rhodocallis elegans Kuetz.	—	—	x	—	"
Metagoniolithon charoides (Lamour.) W. V. Bosse	x	—	—	(*d*)	In deep pools
Platysiphonia sp.	x	—	—	(*d*), (*e*)	Grows on *Pterocladia*
Callophyllis lambertii (Turn.) Grev.	—	—	x	(*d*)	
Pleonosporium comatum (J. Ag.) De Toni	—	—	x	(*d*)	
Neomonospora sp.	—	—	x	(*d*)	
Lophurella periclados (Sond.) Schmitz.	—	—	x	(*d*)	
Centroceros clavulatum (Ag.) Mont.	—	—	x	(*b*)	On *Brachyodontes*
Perithalia inermis (R. Br.) J. Ag.	—	—	x	—	In wrack
LICHENS					
Lichina confinis (Muell.) Ag.	xx	x	xx	(*a*), (*b*)	
Verrucaria sp.	—	—	xx	(*a*), (*b*)	See page 116
PHANEROGAMS					
Cymodocea antarctica	x	x	x	(*e*)	

III. A REVIEW OF THE BIOGEOGRAPHICAL PROVINCES OF TEMPERATE AUSTRALIAN SHORES

Before reviewing the geographical implications of the present survey it is necessary to clarify one point. Since points of the compass have been used in naming two Australian States, some confusion may arise in discussions on distributions unless care is taken. In this paper the words: "South Australian coast" mean the coast of the State of South Australia. If a species ranges from Victoria, through South Australia, to southern Western Australia, the words "southern coast of the continent" or "whole southern coast of Australia" will be used.

(*a*) *Review of Literature*

The present survey of the Victorian coast together with the previous survey of the New South Wales coast (Dakin, Bennett, and Pope 1948) has provided an adequate basis for discussion of the biogeography of temperate Australian shores. Also information is available on zonation of parts of South Australia (Edmonds 1948; Womersley 1947, 1948), parts of Tasmania (Guiler 1950, 1951), southern Queensland (University of Queensland, Science Students' Association 1946, 1947; Hynd 1948), and Western Australia (personal communications from Mrs. B. Marsh and Miss D. Choules).

No attempt will be made to discuss the biogeography of northern Queensland, Northern Territory, or north Western Australia since there is practically no information available on the intertidal zonation of that area. Something, however, is known of the distributions of molluscs and echinoderms, and upon the basis of these data the Solanderian and Dampierian Provinces were proposed by Hedley (1904, 1926) and agreed to by Clark (1946). To these Whitley (1932) added a Banksian Province for the coast of Queensland inside the Great Barrier Reef. The first two of these provinces have been included in Figure 5 but no claim is made as to the validity of their existence or extent.

In the following discussion of the temperate shores, only such tropical species as invade more southerly latitudes in temperate waters will be mentioned.

Few past workers on biogeographical provinces of the Australian littoral have discussed the evidence presented by more than one of the major animal groups, e.g. Tenison-Woods (1876, 1879, 1881), Hedley (1904), Iredale (1914, 1924), Ashby (1926), and Allan (1950), who dealt with the molluscs, and Clark (1938, 1946) with echinoderms. Nevertheless, there seems to have been a remarkable agreement among them, with the exception of Ashby, as to the number and extent of the geographical provinces round the Australian coast. A comprehensive summary of most of their opinions appears in Clark's (1946) account of the Australian Echinodermata, which, however, omits mention of the work of Ashby and Whitley.

As a result of studying the Polyplacophora (chitons) Ashby (1926) proposed a modification of Hedley's four provinces. Ashby's Peronian Province extended from Twofold Bay in southern New South Wales to Keppel Bay in Queensland. His Adelaidean (now known as the Flindersian (Cotton 1930)) Province stretched from "Bass Strait, along the whole of the southern coast of the continent, and up the coast of Western Australia as far as Cape Naturaliste". He proposed a new Tasmanian Province since, in his opinion, there were enough species of chitons confined to the shores of that island to warrant it. However, before Ashby had proposed the new Tasmanian province, Iredale and May (1916) had recognized a distinctive molluscan fauna in south-eastern Tasmania, and had called it the Maugean Region.

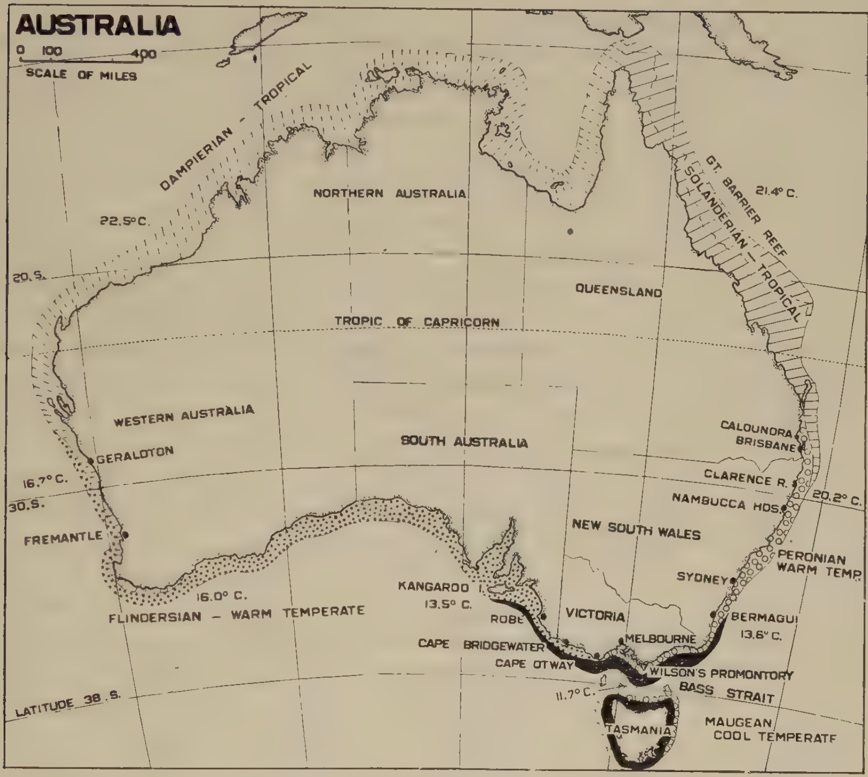
AUSTRALIA
0 100 400
SCALE OF MILES
DAMPIERIAN - TROPICAL
NORTHERN AUSTRALIA
22.5°C.
20.S.
GT. BARRIER REEF
SOLANDERIAN - TROPICAL
21.4° C.
QUEENSLAND
TROPIC OF CAPRICORN
WESTERN AUSTRALIA
SOUTH AUSTRALIA
GERALDTON
16.7° C.
30.S.
FREMANTLE
CALOUNDRA
BRISBANE
CLARENCE R.
NAMBUCCA HDS.
20.2° C.
NEW SOUTH WALES
PERONIAN WARM TEMP.
SYDNEY
16.0° C.
FLINDERSIAN - WARM TEMPERATE
KANGAROO I.
13.5° C.
ROBE
VICTORIA
BERMAGUI
13.6° C.
MELBOURNE
CAPE BRIDGEWATER
CAPE OTWAY
WILSON'S PROMONTORY
BASS STRAIT
11.7° C.
LATITUDE 38 S.
TASMANIA
MAUGEAN COOL TEMPERATE

Fig. 5.—Map of the biogeographical provinces of the Australian littoral on exposed coasts. Tropical biotas are hatched with approximately parallel lines, warm-temperate ones by circles and dots, and cool-temperate ones are solid black. Question marks on the west coast of Tasmania indicate lack of data on the fauna and flora. Minimum winter temperatures are included and appear opposite the part of the coast where they were recorded. The tropical provinces are after Hedley (1904) and are reproduced here without prejudice. See text for further explanation.

Notable exceptions to the authors who considered only single groups of animals are Ekman (1935) and Fischer (1940). Ekman considered evidence from several groups of animals and, apparently working chiefly from literature, divided the Australian littoral fauna into two sections. He described a northern tropical and subtropical zone which extended from approximately the latitude of Sydney in the east (33° 5′ S.) northwards round the continent to Geraldton (28° 47′ S.) in Western Australia. The southern part of the continent he believed to support a warm-temperate fauna. He suggested that the latter contained the truly endemic Australian elements. Ekman dealt with the fauna of the shallow seas as well as with the intertidal animals, and allowance must be made for this fact.

Fischer's account added few new facts and he did not suggest any amendments to the arrangement of the biogeographical provinces already put forward (see his text figure 1).

Stephenson (1948) found it necessary to modify Ekman's scheme of biogeographical provinces for South Africa and (1948, Plate 15) produced a new map of the biogeographical provinces for the southern hemisphere, based on his own and Ekman's data. He expressed doubts as to the validity of Ekman's scheme for Australia.

In a brief account of a survey of some of the more important intertidal algae in Australia, Newton and Cribb (1951) did not specifically mention Victoria although Tasmanian shores received attention. Their remarks are relevant and their findings are as follows: there is a resemblance between the algal floras of New South Wales and the southern coast of the continent in South Australia and round into Western Australia. In both these areas *Ecklonia radiata* is found in the lowest part of the intertidal, and *Sargassum* spp. and *Cystophora* spp. also occur. Whereas *Cystophora* spp. are prominent in South and Western Australia, they are not so in New South Wales, and *Phyllospora comosa* seems to replace them to a large extent. The presence of a giant fucoid, *Sarcophycus potatorum*, and of the giant kelp *Macrocystis integrifolia* is noted in the infra-littoral in Tasmania, and at a higher level, a marked growth of the brown alga *Splachnidium rugosum*.

The survey by the present authors has demonstrated the importance of *Sarcophycus*, *Macrocystis*, and *Splachnidium* along the Victorian coast so that its resemblance in this respect to the shores of Tasmania is obvious. It is thus evident that the Victorian flora, like the Tasmanian one, differs from those of the coasts either west of Robe, S.A., or north of Bermagui, N.S.W., to a quite marked extent—especially in the infra-littoral part of the shore.

(*b*) *Method of Determining Geographical Provinces*

In this paper the authors take into account the distributions of as many groups of intertidal animals and plants as possible in delineating geographical provinces. Following the example of Stephenson (1944) only distributions of organisms on the exposed coasts have been used to determine the limits of provinces and those from inlets, bays (such as Port Phillip and Western Port), or estuaries are neglected.

The data come partly from the two detailed surveys of over 2,000 miles of coast made by the authors, and partly from the other modern sources (see first paragraph, Section III (*a*)).

Allee (1932) records the fact that a higher proportion of species representative of warmer waters are found on flats in shallow inlets at Woods Hole than in the fauna of neighbouring exposed coasts where the summer temperatures are less extreme. He pointed out that on the flats (sheltered, inshore waters) only 11 per cent. of the common animals taken over a period of 2 years were species from colder waters, while in locations nearer deeper water, where the highest temperature was 9°C. colder than that over the flats, 50 per cent. of the shore species were of the colder, north-ranging species.

It is obvious that here species normally inhabiting warmer seas can extend their geographical ranges into colder latitudes by living in inlets where waters are shallow, with the consequent effect of the warming in summer of the water lying over the flats.

Observations made by the present authors show that this same phenomenon of distribution occurs in Australia. On the east coast, for example, there is a well-grown bank of corals growing near Myora, Stradbroke I., in Moreton Bay, Queensland. Associated with it are a number of other tropical species (University of Queensland, Science Students' Association 1946). This coral lies well to the south of any equally rich growth on the exposed coast of Queensland. On the eastern side, exposed to the ocean, of this same island, Hynd (1948) does not find corals or alcyonarians in the lowest intertidal level at Point Lookout.

Another similar case is that of the chiton *Liolophura gaimardi* (Blainville) but in this instance the nature of the distribution has been obscured in systematic literature. According to Iredale and Hull (1927), *Liolophura queenslandica* Pilsbry inhabits the open coast from Trial Bay, N.S.W. (latitude 30° 56′ S.), north into Queensland. Another species, *L. gaimardi* (Blainville), has a peculiarly restricted range, being found in Pittwater, Port Jackson, and Port Hacking, three inlets in the vicinity of Sydney.

These two species are so closely similar that the present authors could find no difference whatever between them. Iredale (personal communication) stated that *L. queenslandica* and *L. gaimardi* had been separated only because of this break of some 250 miles between their two ranges and because one occurred on the open coast whilst the other was in inlets. In other words one would have to know the locality to name the species. It is felt that this is typical of the numerous cases where a species has retired into sheltered, shallow waters at the end of its range, and that *L. queenslandica* is a synonym of *L. gaimardi*.

In Port Jackson, which was exhaustively collected in the past, a number of tropical invertebrates have been found. Hedley (1915, pp. 26, 27) postulates a change in climate in recent geological times to account for some of these distributions. It is felt, however, that these may be yet other examples of the type of distribution cited above but, until a survey is also made of estuarine and inlet faunas along the whole coast, this problem must remain unanswered.

Similar in their behaviour are a number of typically warm-temperate species of molluscs. Several species common on the open coast in New South Wales are absent from the intertidal of the exposed coast in Victoria but, according to the literature, are found in Western Port or in the entrances to the coastal lagoons behind Ninety Mile Beach. These instances have been quoted to justify the exclusion of estuarine faunas from the main discussion.

(*c*) *Analysis of the Australian Temperate Fauna and Flora*

Four distinct geographical components may be recognized as follows: (i) a small tropical component; (ii) a warm-temperate one; (iii) a cool-temperate, and (iv) a universal component which occurs in the intertidal region along most of the coastline south of latitude 30° S.

(i) *The Tropical Component.*—Round the northern half of the Australian coastline subtropical or tropical elements dominate the intertidal zone. The tropical region is marked by the presence of coral reefs or of reef-building species attached to a rocky substratum in the lowest tidal areas, or by other equally characteristic species. While a few tropical organisms are occasionally collected as far south as Sydney or even Shellharbour (lat. 34° 36′ S.) this might be expected in view of the prevailing current system. The east Australian or Notonectian current sets from the north and probably brings with it from tropical waters the planktonic or young stages of a number of northern species. Whilst a few of these can, and do, survive at odd points along the coast of New South Wales where the environment is specially favourable, they rarely become prominent features of the intertidal zonation and generally depend on immigrants from the north to maintain their populations. Thus Trial Bay, Norah Head, Long Reef near Sydney, and Shellharbour are four localities known to the authors where tropical species may be taken at certain times of the year. In between these places, long stretches of the coast occur where tropical invaders are absent and so the greater part of the intertidal biota of New South Wales is basically of a warm-temperate type.

After examining all available data it was felt that Ekman's boundary on the east coast between tropical and warm-temperate zones was placed too far to the south, and most other authors on biogeography to whose work reference has been made, agree. There is no area of coast known to the present authors in the 500-600 miles north of Sydney, in fact till approximately latitude 26° S. is reached, near Noosa Heads, Queensland, in which enough tropical species regularly occur in the intertidal zone to give it a truly subtropical rather than a warm-temperate character.

At the latitude of Nambucca Heads (30° 39′ S.), the beginnings of a subtropical fauna and flora appear in the intertidal zona and a few corals, two species of zoanthids, and several tropical species of algae, including *Halimeda*, may be found sporadically. Further to the north, near the mouth of the Clarence River (lat. 29° 25½′ S.) many additional tropical species of crustaceans, molluscs, and holothurians may be taken regularly in the lowest intertidal zone. It is not, however, till north of Noosa Heads (lat. 26° 35′ S.) that the intertidal flora and fauna is truly subtropical. At Caloundra (lat. 26° 49′ S.) the present authors found corals, zoanthids, and alcyonarians such as *Xenia* sp. as well as tropical echinoderms and molluscs, forming marked features of the intertidal scene, and the dwarf kelp *Ecklonia radiata* and the ascidian *Pyura stolonifera*, which are such typical markers of the temperate zone, were very sparse in their occurrence.

The truly tropical provinces may be said to end at the southern end of the Great Barrier Reef and its outlying groups of islands.

Some of the more outstanding tropical species which appear sporadically along the coast of New South Wales are molluscs and echinoderms, though a few corals, zoanthids, and tropical algae may be found. Corals such as *Plesiastraea urvillei* E. & H., and zoanthids, including *Palythoa australiensis* Carlg. (1950*a*, 1950*b*), may be found at Woolgoolga (south of the Clarence River) or even as far south as Nambucca Heads (though here in a large, permanent, high rock pool). Here also algae of the genera *Halimeda* and *Caulerpa* may be collected. From Angowrie, a little further to the north, collections in the Australian Museum show 18 tropical species of nudibranchs (Allan 1947), and numerous other tropical gastropods; 23 tropical crabs, and 10 tropical echinoderms (including four large-sized species of holothurians), all of which were collected between tide marks. During collecting here under unfavourable conditions, the present authors took 20 tropical species. Sea urchins such as *Tripneustes gratilla* (Linné), *Echinometra mathei* (de Blainv.), *Diadema setosa* (Leske), appear quite frequently in the far north of New South Wales, and *Tripneustes* may occur as far south as Sydney in the summer. The large black holothurian *Holothuria leucospilota* (Brandt) occurs quite plentifully from Angowrie north into the tropics. Prominent tropical molluscan species seen invading the waters of northern New South Wales include the chiton *Liolophura gaimardi* (Blainville), *Turbo militaris* Reeve, *Strombus luhuanus* Linné, and three or four species of cowries which may be collected as far south as Sydney or even at Shellharbour. In addition to these common, obviously tropical forms there must be many additional smaller species which could be cited here especially among the polychaete and polyclad worms and small molluscs. As has already been mentioned, the tendency appears to be for these tropical species to be concentrated in various small, circumscribed areas at intervals along the coast from north to south. Probably they occur where eddies of warm Tasman or Notonectian current touch the coast.

In the western warm-temperate province, the records of collections made by Mrs. Marsh and Miss Rutt during their ecological survey of the Western Australian coast show similar distributions for such typically tropical species as the sea urchins *Echinometra mathei* and *Tripneustes gratilla*. They are regular members of the fauna at Ganthaeume Bay (lat. 27° 40′ S.) but occur sporadically south of this, turning up, for instance, at Rottnest I., near Fremantle, or Garden I. just to the south. At Rottnest other tropical species are also found, e.g. zoanthids, corals, and alcyonarians among the animals, and *Halimeda* sp. among the algae.

The tropical component is absent in Victorian and Tasmanian waters and this constitutes one of the differences between the warm- and cool-temperate provinces.

(ii) *The Warm-temperate Component.* — The animals considered typical of the eastern warm-temperate or Peronian fauna include the barnacles *Tetraclita rosea,* where exposure is maximal, and *Balanus imperator* Darwin where exposure is considerably less. Both these species extend their ranges north of the area covered by the authors' survey but it is known that in both northern Queensland and Western Australia *Tetraclita squamosa* (Brug.) dominates the intertidal rocks rather than *T. rosea*. *T. rosea* occurred only on the extreme east coast of Victoria.

Characteristic warm-temperate echinoderms are the seastars *Asterina inopinata* Liv. and *Patiriella gunii* (Gray); the echinoids *Heliocidaris erythrogramma* (Val.) (which occurs intertidally), *Holopneustes pycnotilus* Clark, and *Centrostephanus rodgersii* (Agassiz), which ranges from Norah Head to Eden, N.S.W., and a fourth species *Heliocidaris tuberculata* (Lamarck), which has an even more restricted range from Smoky Cape to just south of Sydney. The last two species are both found (the latter very common) at Lord Howe I., which lies about 300 miles due east of Port Macquarie, N.S.W.

The following chitons occur only in the Peronian or eastern warm-temperate province: *Sypharochiton septentriones* (Ashby), *Cryptoplax mystica* (Iredale and Hull), *Haploplax lentiginosa* (Sowerby), and *H. smaragdina* (Angus), though the range of the last-named does slightly overlap into eastern Victoria. The *Poneroplax* species in New South Wales known as *P. paeteliana* (Thiele) is smaller in size than its Victorian counterpart, *P. albida*.

The turban shell *Ninella torquata* (Gmelin) marks the warm-temperate waters, its counterpart in the west being *N. torquata* subsp. *whitleyi*. The thaid, *Dicathais orbita* (Gmelin) of New South Wales has pronounced and regular grooving on its heavy shell. The corresponding shell in Victoria and South Australia, *D. textiliosa*, has much finer sculpturing and grooving. In Western Australian waters, the related shell *D. aegrota* (Reeve) has lost most of the grooving and the sculpturing takes the form of rows of large knobs. When a series of these shells from numerous localities between Western Australia and New South Wales is examined, they appear to form a cline with every intergrade of sculpturing between all three "specific" forms.

Other molluscs in the Peronian province are *Nodilittorina tuberculata* (Menke) and the two nudibranchs *Flabellina ornata* (Angus) and *Casella atromarginata* (Cuvier).

Crustaceans which are confined to warmer shores are the crabs *Pachygrapsus transversus* (Gibbes) and the swift shore species, *Leptograpsus variegatus* (Fabr.). The latter ranges south to Mallacoota in the east, is absent along the rest of the Victorian coast, but reappears in South Australian and Western Australian shores.

The band of the ascidian *Pyura stolonifera* is absent from shores in western Victoria but very prominent right up the coast of New South Wales and at a few odd points along the rest of the Victorian coast. It is probably more a warm-temperate than a cold-temperate species though it ranges into cooler waters.

The western warm-temperate or Flindersian Province shares many species in common with the Peronian one or is typified by nearly related species. Among the echinoderms, the sea urchin *Heliocidaris erythrogramma* occurs intertidally and the asteroid *P. gunnii* is identical with the New South Wales form. There are two species of *Holopneustes* — *H. porossisimus* (the Flindersian counterpart of *H. pycnotilus*) and *H. inflata*. These two Flindersian urchins range into Victoria as far east as Waratah Bay and will be commented upon later.

Characteristic common chitons of the Flindersian area are *Clavarizona hirtosa* (Blainv.), which is probably the counterpart of *Liolophura gaimardi* (Blainv.) in New South Wales and therefore a tropical species. Our present records of it extend west and north only to Gantheaume Bay and till its range is extended into the tropical biota it seems better to list it here.

There is a western counterpart of the eastern *Onithochiton quercinus* (Gould). It looks similar but is called *O. occidentalis* Ashby, and ranges from Ganthaeume Bay south to Garden I., near Fremantle. It is probably a tropical invader also but its northern limit is not known although it does not occur in Northern Territory (Ashby 1926).

The grapsoid crab *Leptograpsus variegatus* is also found in the west but is absent from most of the Victorian coast and is not recorded from Tasmania although a search was made for it (Tweedie 1942). The peculiar pagurid *Cancellus typus* H. Milne Edw., which lives in a hollowed-out stone, occurs in both the Peronian and Flindersian provinces but not in

Victoria. The Flindersian supra-littoral has a littorinid, *Tectarius rugosus* (Menke), which differs only slightly from the Peronian *Nodilittorina tuberculata* in spite of the different generic names.

There are no barnacles which characterize or particularly mark the Flindersian region.

The algae are less developed in the warmer waters and less of a feature on intertidal rocks in the warm-temperate provinces than in Victoria and Tasmania. Newton and Cribb (1951) have commented on the paucity of littoral species in Australia as compared with Britain. *Ecklonia radiata* is a dominant infra-littoral alga both in the Peronian and Flindersian provinces whereas it is of minor importance in Victoria. In New South Wales, another prominent brown alga is *Phyllospora comosa,* and it too plays a less important part in the Victorian infra-littoral. *Phyllospora* is not recorded in the west but certain species of *Cystophora* occur there and while these same species of *Cystophora* may occur in Victoria, there are certain species among them, e.g. *C. torulosa,* which have a restricted range in Victoria and Tasmania. The coralline *Amphiroa anceps* (Lamk) Decne is prominent in the Peronian Province and was not recorded intertidally in Victoria. Other major variations in algal distributions have already been commented upon in the review of literature.

To sum up, it will be evident that there are distinct breaks in the distributions of a number of the typical species of warm-temperate algae and animals. These breaks occur generally in the vicinity of Bass Strait and if, as Ekman (1935) postulates, the Australian shore fauna originated in the tropics and migrated southward—each species according to its ability to withstand increasing cold and other linked changes in the environment—the basic similarity of the two warm-temperate faunas is understandable. They might well have originated from a common stock and the differences that may be seen would then have appeared as an effect of isolation, since they are cut off from one another in the north by the tropical fauna and in the south by a not very extensive area populated by cooler-water species.

(iii) *Cool-temperate Component.*—Stephenson (1948, p. 227) has remarked that the cool-temperate biota in South Africa has giant brown algae marking the infra-littoral fringe and that these are not encountered either in the warm-temperate or tropical provinces. Only in the cool-temperate province in Australia are giant brown algae found, and in addition there are a number of species of animals which are characteristically more cool- than warm-temperate, although in some cases they range a short distance along the warmer parts of the coast.

Algae characterizing the cooler waters in Victoria are the giant fucoid *Sarcophycus potatorum* and the kelp *Macrocystis integrifolia* in the infra-littoral fringe. The littoral area of the rocks is marked by the presence of sheets of mussels of various species, and at certain times of the year, in the lower part of the barnacle zone, by a band of the alga *Splachnidium rugosum*. The brown alga *Cystophora torulosa*, in the lowest part of the littoral or in the infra-littoral, is also characteristic. The barnacle *Tetraclita rosea*, which is a marked feature of this zone in the eastern warm-temperate area, is absent. On the Victorian coast the chitons found on exposed rocks (neglecting those in the cryptofauna) are reduced to one or two species of the genus *Poneroplax*, whereas in the warm-temperate area three or more genera are represented. In Tasmania, both on the east and west coasts, a southern variant of one of the New South Wales species, *Sypharochiton maugeanus* Iredale, appears in addition to the species of *Poneroplax*. *Sypharochiton* was not found in Victoria.

In the supra-littoral, the littorinid *Melaraphe praetermissa* appears on cool-temperate shores whereas *Nodilittorina tuberculata* or *Tectarius rugosus*, so prominent in warmer regions, are absent. Also the crustacean fauna of this highest part of the shore is characteristic. *Ligia australiensis* and several other isopods occur in thousands on the open coast in suitable localities in Victoria, and the crabs *Brachynotus octodentatus* and *Paragrapsus quadridentatus* replace entirely the common grapsoids of the warm-temperate province, *Leptograpsus variegatus* and *Pachygrapsus transversus*. There is also a prominent growth of dark-coloured lichens (either *Lichina confinis* or *Verrucaria* sp.) on this part of the shore.

Some prominent species which characterize this geographical province are the gastropods *Melaraphe praetermissa*, *Notoacmea mayi*, *Conacmea alta*, *Lepsiella vinosa*, *Cominella lineolata*, and *Siphonaria diemenensis*; and the echinoderms *Tosia australis*, *Nectria ocellata*, both of which are common, and also *Austrofromia polypora*, which is rarer but, like the two foregoing species; occurs intertidally. Another common asteroid is *Patiriella brevispina* which, according to Clark (1938), is a colour variation which also shows slight but constant differences from *P. gunnii*, its counterpart in warmer seas. *P. brevispina* is also found in the south-west of Western Australia (King George Sound) and in one or two localities in South Australia. The small black or blue-black holothurian *Mensamaria thomsoni* is also numerous in places where shelter offers. Crustacea which are characteristic include *Paramithrax latrielli*, *Paragrapsus quadridentatus*, *Brachynotus octodentatus*, *Lomis hirta*, and the amphipod *Talorchestia? diemenensis*.

Since the cool-temperate fauna has been dealt with at length in Section II, a discussion is now given of the universal component in the temperate fauna and of some variations in distributions of species common to both temperate areas.

(iv) *The Universal Component.*—Some species occur throughout Australian temperate waters and some have a wide distribution in the southern hemisphere. A few even extend into more tropical waters.

Amongst the most prominent are the following:

Algae: *Hormosira banksii, Colpomenia sinuosa, Gymnosorus variegatus, Pterocladia capillacea*

Mollusca: *Cellana tramoserica, Patelloida alticostata, Patellanax squamifera, Subninella undulata, Melanerita melanotragus, Melaraphe unifasciata, Bembicium melanostoma, Austrocochlea obtusa*

Echinodermata: *Patiriella calcar, P. exigua, Coscinasterias calamaria, Heliocidaris erythrogramma*

Brachyura: *Plagusia capensis*

Cirripedia: *Catophragmus polymerus, Chamaesipho columna, Balanus nigrescens*

Annelida: *Galeolaria caespitosa*

Actinaria: *Actinia tenebrosa, Oulactis muscosa, Cnidopus verater.*

(*d*) *Comments on some Distributions and Variations of Temperate Species*

Gislén (1943) working on the Californian coast, noticed that: "at different latitudes, there occurred vertical displacements of the same community, a phenomenon which, as far as I am aware, has never before been either stated or investigated". Allee (1932) had previously stated: "near the extremes of their geographical range, animals can live in deeper water more readily than along the shallow margins where the temperature changes are great", and had quoted examples.

Similar distributions have been noticed by the present authors. For instance, (1) *Hormosira banksii* occurred at a lower level in Victoria and in the far south of New South Wales; (2) the asteroids *Nectria ocellata* and *Austrofromia polypora* were always found above low-water mark of spring tides in Victoria but were taken by trawlers in deeper water off the southern coast of New South Wales and along the southern coast of the continent to southern Western Australia. Whilst Clark (1938, 1946) recorded the finding of odd specimens of these species between tide marks in Victoria, he expressed doubts as to their authenticity—considering them exceptional; (3) the echinoid *Heliocidaris erythrogramma* which Clark referred to (1946, p. 329) as "the most common regular sea urchin from Port Stephens, New South Wales, along the southern coast of Australia to the Abrolhos Islands and Shark Bay on the western side of the continent", occurs differently in Victoria. In New South Wales, and in the Flindersian Province, it was chiefly intertidal but was rarely (never) found at this level in Victoria. There it occurred just below low-water mark of spring tides, in much more sheltered situations.

Constant structural differences could be observed in specimens from the two regions. The Victorian specimens resemble closely those from Western Australia which Döderlein (1914) named *H. hartmeyeri.* However, Clark (1938) thought that this latter was merely a variant of *H. erythrogramma. H. hartmeyeri* ranges from Shark Bay in Western Australia to Tasmania and Victoria and, in view of the present findings in Victoria, if this type of urchin is constantly found subtidally, it may be advisable to retain Döderlein's name as a subspecies.

A similar case occurs in the seastars, where *Patiriella brevispina* H. L. Clark has been accorded full specific differentiation by Clark from the very similar *P. gunnii* (Gray). The latter is common intertidally on the New South Wales coast and along much of the Western Australian coast and has a variable colour pattern with greens and greys predominating. In the extreme south of Western Australia and at places on the southern coast of the continent to Victoria, a very similar species appears in suitable localities, the colour of which is constantly a rich purple-brown with orange tube-feet. Clark initially regarded this as a colour variant of *P. gunnii,* but finally gave it full specific rank. *P. brevispina* may well be regarded as the cool-temperate variant of the similar warm-temperate species.

The tendency of tropical species to enter estuaries at the end of their ranges has been commented on previously. This type of distribution has also been noted among species from the cool-temperate province, some of which retire to sheltered coasts at the northern or warmer extremity of their range. The pulmonate *Siphonaria diemenensis* and the isopod *Ligia australiensis,* for instance, are found inside Sydney harbour though on the ocean coasts of New South Wales or Victoria their ranges end well to the south of this point.

Some of the mollusc species occurring in both warm- and cool-temperate zones show slight but constant colour differences in the two areas. For instance, the very common and variable periwinkle, *Austrocochlea constricta* (Lam.), is larger in Victoria and the uneroded shell is generally light grey. In New South Wales the shell is generally black, marked with irregular white stripes (of variable thickness) or flecks, and only when eroded are the inner shell whorls of the Peronian species coloured like the uneroded Victorian shell. The outer whorl always remains dark.

A recent detailed study has been made of the genus *Austrocochlea* by Liddell (1950), and the ranges of the various subgroups she proposed for this genus agree well with the geographical provinces proposed by the present authors.

The common intertidal littorinid *Bembicium melanostoma,* which is smaller in Victoria and more like the juvenile of the New South Wales species, has received the specific name of *B. nanum.* Careful examinations by Miss Hope Macpherson of the National Museum of Victoria have failed to show significant differences between the two groups.

Iredale (1924) considered the shells of the fissurelid *Montfortula* from Port Fairy, Vic., to be *M. rugosa* (Q. & G.) since they differed slightly from the New South Wales and eastern Victorian specimens known as *M. conoidea.* The range of *M. rugosa* was given as from Port Fairy to Busselton, W.A. Actually this form extends eastwards to Cape Otway and seems to grade into the *M. conoidca* type. Again Miss Macpherson saw no reason to differentiate between the two.

In Section III (*c*), mention has been made of the geographic variations to be seen in *Dicathais* and *Ninella,* two of the common large intertidal gastropods.

Considerable variation in the limpet, *Patellanax squamifera,* has been noticed and three different shell types could be recognized in Victoria alone, one of which was referred to as *P. peroni* (Blainv.). These three kinds intergrade so much, however, that they are regarded here as all one species, *P. squamifera.*

It is felt that some comment is necessary on Fischer's statement on *Brachyodontes*: "ce nom suprendra peut-être les auteurs australiens, qui ont noté dans la région flindersienne la présence de *B. erosus* et de *B. rostratus,* ce dernier 'at half tide' suivant Cotton et Godfrey (1938, p. 119). Je ne trouve pourtant aucune différence entre des *Brachydontes* qui j'ai récoltés à Outer Harbour et *B. variabilis,* Krauss, de la Mer Rouge et de la région indo-pacifique." It has been noticed in the present work that the type of *Brachyodontes* known as *erosus* has been collected in localities past which a swift current flows, e.g. islands in the Kent and Furneaux groups at the eastern end of Bass Strait. On nearby shores of Tasmania and Victoria, *B. rostratus* is found. It is therefore conceivable that the *erosus* form is due to some factor or factors in the environment. However, until Fischer's statement has been tested by reliable conchologists, it is proposed to continue with the names current locally.

Some comment on the size of the Victorian chitons of the genus *Poneroplax* is also required. Two species are found, *P. costata* and *P. albida,* of which the former is not recorded east of Walkerville in Waratah Bay. *P. albida* shows very little difference other than that of size from *P. paeteliana* (Thiele) of the Peronian Province. Again, in Miss Macpherson's opinion, there was little difference between these two species other than differences due to excessive size of *P. albida,* and it is felt they may turn out to be geographical forms of the one species (see Gislén 1943).

Differences were also observed in the cirripedes *Ibla quadrivalvis* and *Chamaesipho columna. Ibla* was associated with *Galeolaria* and with *Brachyodontes* but whether it occurred at the higher or lower level on the rocks it was consistently larger than it was in New South Wales. The same applied to *Chamaesipho* which, although often much sparser per unit area in Victoria, was nevertheless almost twice as tall as its Peronian counterparts.

From Guiler's account (1950), the occurrence of the lichen band is slightly different in Tasmania from that found in Victoria. According to him, the band of lichen appears in the upper part of the littoral. This fact is confirmed, so far as *Lichina confinis* is concerned, by Mr. A. B. Cribb (personal communication). In Victoria it is definitely situated in the *Melaraphe* zone and can extend its vertical range into the supra-littoral in localities exposed to the influence of continual fine spray, e.g. at Warrnambool, Nelson Bay, and Cape Bridgewater.

Finally some comment must be made on the fact that an echinoid which appears to be intermediate between *Holopneustes pycnotilus* and *H. inflatus* appears in Table 2. Clark (1938, p. 394) noted intermediates between *H. porosissimus* and *H. inflatus* in the vicinity of Cape Leeuwin, W.A. Of these *H. porosissimus* ranges throughout the whole of the Flindersian Province and into Victoria and Tasmania, while *H. inflatus* has a more restricted range from Fremantle along the whole southern coast to Victoria and Tasmania. The fact that intermediates between this latter species and the typically Peronian *H. pycnotilus* occur in Victoria, where their ranges overlap, is extremely interesting. All three species, which differ quite distinctly from one another, may be found in Victoria and Tasmania in addition to the particular intermediate listed here.

IV. Conclusion

Extent of the cool-temperate (Maugean) province

It has been shown that the fauna and flora of the intertidal part of the shores of Victoria differ considerably from those of New South Wales and also from those of the western warm-temperate or Flindersian Province.

As one proceeds southwards from Sydney on the coast of New South Wales it can clearly be seen that certain colder-water species of algae, crustaceans, bivalves, and gastropods begin to appear in the intertidal zone and to be represented in significant numbers the further south one proceeds. For example, the mussel *Brachyodontes rostratus* forms large clusters in favourable places from Tuross Heads (lat. 36° 10′ S.) southwards. South from Bermagui (lat. 36° 18½′ S.) the giant fucoid *Sarcophycus potatorum* almost completely replaces *Ecklonia radiata* and *Phyllospora comosa* in the lowest intertidal area, and at Bastion Point, Mallacoota (just south of the Victorian border), the kelp *Macrocystis integrifolia* appears in the upper part of the sublittoral. From this point southwards a number of species of gastropods, e.g. *Cominella lineolata, Lepsiella vinosa,* and *Siphonaria diemenensis*, and crustaceans such as *Lomis hirta* and *Paragrapsus quadridentatus,* to mention only a few selected species, appear regularly in the fauna of the exposed coast.

As significant as the invasion of colder-water species is the scarcity or absence altogether in these southern latitudes of the east coast of such prominent warmer-water species as *Onithochiton quercinus, Sypharochiton septentriones,* the gastropod *Morula marginalba,* and the barnacles *Tetraclita rosea* and *Balanus imperator.* These species disappear almost completely south of Bermagui, and whilst one or two specimens of *T. rosea* may be collected as far south as Mallacoota, none was found at Wilson's Promontory nor is it recorded from Tasmania.

In the same way, as one proceeds eastwards through the Flindersian Province from Cape Leeuwin, W.A., one after another of the prominent cool-temperate species appears. The information on distributions in this region is, as yet, scanty and what is available to the present authors has come from personal communications (already quoted).

Brachyodontes rostratus, which is not a dominant shore form in south Western Australia (cf. field notes of Mrs. Marsh and Miss Choules), is also not mentioned by Edmonds in a personal communication on the zonation at Everard, at the eastern end of the Great Australian Bight. However, Edmonds (1948) records it at Kangaroo I., so that it must range westward to some locality between these two points (unless Kangaroo I. marks the western end of its range).

Splachnidium rugosum is recorded from Kangaroo I. by Womersley and is not at present recorded from Western Australia. The giant algae *Sarcophycus* and *Macrocystis* are recorded at Robe (lat. 37° 10½′ S. and long. 139° 45½′ E.), and also the littorinid *Melaraphe praetermissa.* Thus the conditions found in the south of New South Wales are repeated in the eastern part of the Flindersian Province.

Because of the prominence of the cool-temperate element in Victoria it is proposed to offer for consideration a new arrangement of the biogeographical provinces round the southern half of the Australian continent which will take this into account. This arrangement is illustrated in Figure 5. It differs from the previous schemes put forward in that a cool-temperate biota is recognized between and overlapping the two warm-temperate ones at present known as the Peronian (in New South Wales) and the Flindersian (along the southern coast of the continent). It is felt that the hydrological data quoted in the earlier part of this paper are supporting evidence of this new biogeographical element in the Australian intertidal flora and fauna.

Since there is an extensive area of overlap between the two warm-temperate provinces and the cool-temperate one of Victoria, it is difficult to define exactly the boundary of the new region. There is very little sign of cool-temperate influence in shore zoning north of Bermagui, N.S.W., or west of Robe, S.A., and such wanderers from the cool-temperate as do occur tend to be found only in little isolated areas just as were the tropical wanderers along the coast of New South Wales. However, the cool-temperate zonation is more evident in Victoria between Bastion Point, Mallacoota, in the east, and Cape Bridgewater, near the South Australian border in the west.

It is highly probable that the truly cool-temperate region will be found in southern Tasmania when a careful survey of exposed coasts is made there. Iredale and May (1916) first recognized the need for differentiating the molluscan fauna of south-eastern Tasmania from that of the warm-temperate zone of New South Wales and bestowed the name "Maugean

Province" on this area. It is believed that the differences they recorded are probably a mere accentuation of the differences which, to the present authors, are already evident on the Victorian coast to the north, and that these are due to the presence of greater numbers of endemic, cool-temperate species in the Tasmanian intertidal biota.

The only publications on intertidal communities of Tasmanian shores (Guiler 1950, 1951) contain data which it is felt support this theory of Tasmania's position in the biogeographical scheme and nothing which contradicts it. Guiler's first paper dealt only with an area which the present authors consider atypical because of possible freshwater influences and its somewhat sheltered position. Observations on the mainland have been confined to the zoning of fully exposed coasts, and only in his description of transect 7 does Guiler appear to be working in an area where exposure and other physical factors of the environment approach in any way those of the areas described in the present paper.

The above views on Tasmania's biogeographical position are based partly on knowledge of the intertidal algal flora and partly on data gathered from personal inquiries from other biologists and friends who have made observations or brought back collections from various localities. Colour transparencies specially taken for the authors have also been used. The beds of giant brown algae and other smaller species which characterize the Victorian shores are present in Tasmania (Lucas 1915), and also the beds of mussels in the littoral (to mention two of the most outstanding cool-temperate indicators). Judging purely from literature references there are many more, but only extensive field work will clarify this.

It only remains to suggest a name for this new shore province seen in Victoria. Iredale and May (1916) used the name "Maugean Province" for what is evidently a very similar fauna in south-eastern Tasmania, and since several of the mollusc species which they designated as characteristic of it are also found in Victoria, it seems reasonable to extend the use of their name to cover the whole cool-temperate biota described above, and to use it for the flora and fauna of the shores of both Victoria and Tasmania. Hedley's (1926) name "Adelaidean", which has been rejected by later workers in favour of Cotton's (1930) Flindersian, has not been used by the present authors for Victoria because Hedley clearly stated (1904, p. 880) that he applied it to the fauna in the neighbourhood of Adelaide where the fauna had been elaborated by Angus and Tate. It belongs, therefore, to the western warm-temperate area.

Some comment appears to be necessary to explain why such noted workers with detailed knowledge in their respective groups as Hedley (Mollusca), or Clark (Echinodermata), could overlook the presence of so extensive a cool-temperate biota. It is felt that the explanation for this is that it was due partly to the extensive overlapping of the warm- and cool-temperate faunas both on the Victorian and Tasmanian coasts, and partly to the fact that little serious collecting appears to have been done in the past on the fully exposed shores of Victoria.

Judging from the localities in literature, and in museum collections, most of the past collecting in the south has been done in sheltered inlets and bays. Here the flora and fauna can have a very different constitution from that of a neighbouring exposed coast. Species may thus appear in the floral and faunal lists for a given locality and yet be of minor importance in the coastal biota. The safest way to determine geographical subdivisions in the intertidal zone is therefore to make extensive field surveys of the exposed coasts and record not only presence or absence of species but also take note of their relative abundance and importance in the general scheme of zonation.

Hedley (loc. cit.) recognized that there was a change in molluscan fauna somewhere between Twofold Bay, N.S.W., and Western Port, Vic., and advanced the theory that it might be due to the effects of the isthmus which formerly joined Tasmania to the mainland, in the neighbourhood of Wilson's Promontory. He thought this land barrier would make it necessary for any littoral species which migrated from New South Wales to the southern coast of the continent or vice versa, to double the southern tip of Tasmania and thus withstand very much colder sea temperatures than those to which they were accustomed. Species that were not eurythermal would be debarred from free access from one coast to the other. He postulated a certain amount of intermingling of faunas since the removal of the land connexion, but considered the differences in evidence today were probably due to a carrying over of the effects of the former isthmus.

Since current geological opinion gives the minimum time since the destruction of this isthmus as 25,000 years, it is felt that there has been ample time and opportunity for free migration of most littoral species between the coasts of New South Wales and Victoria since that time, and that Hedley's explanation is not enough to account for the facts of present-day distributions. Some factor or factors in the environment which are continually operating today as a barrier between these two areas must be looked for.

It is felt that sufficient evidence to account for the distributions of the animals and the algae today has been given in Section II of this paper, and that the body of cooler water in Bass Strait is an effective barrier separating the two warm-temperate biota known as the Peronian and Flindersian Provinces. The sea temperatures in Bass Strait today are similar to those recorded off the south coast of Tasmania—a fact that Hedley seems to have overlooked.

Whilst future workers may find it expedient to subdivide Australian shores into further provinces for the sake of convenience it is felt that the basic divisions—tropical, warm-temperate, and cool-temperate—will remain much the same as those shown in Figure 5.

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INTERTIDAL ZONATION OF VICTORIAN SHORES

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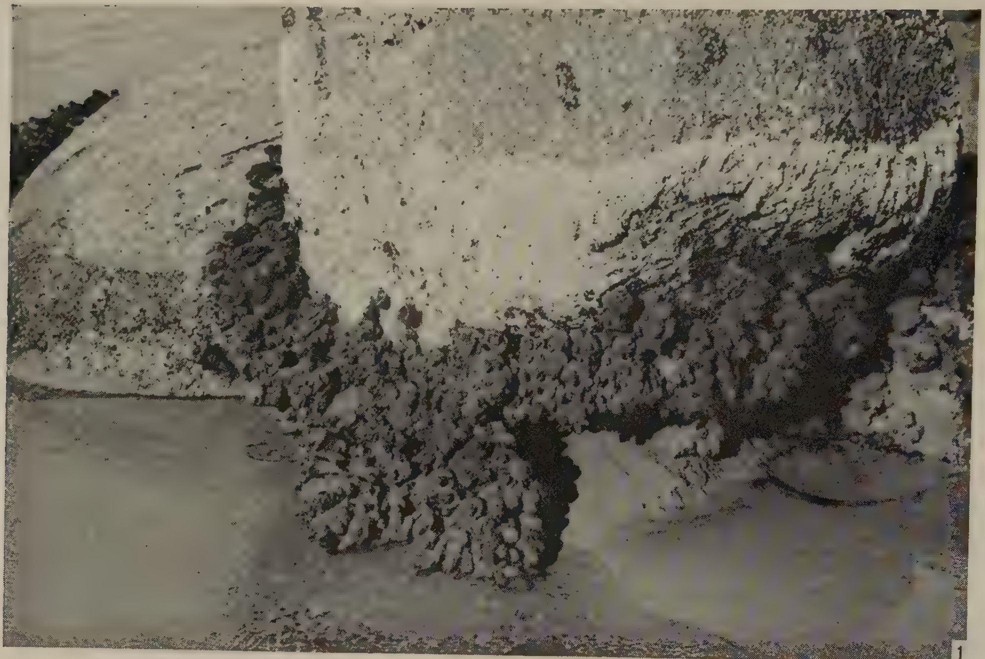
INTERTIDAL ZONATION OF VICTORIAN SHORES



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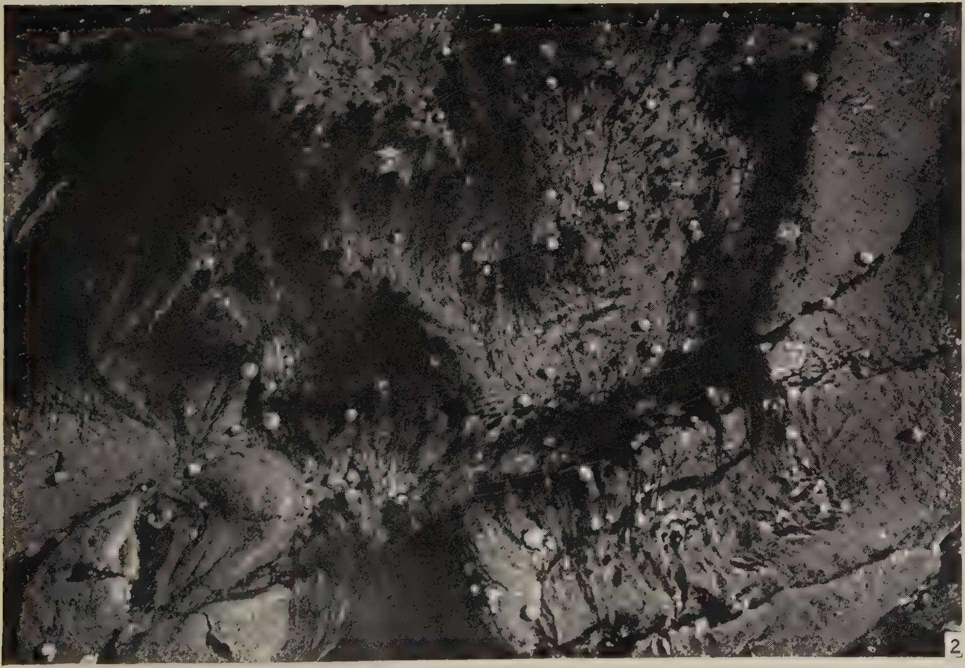

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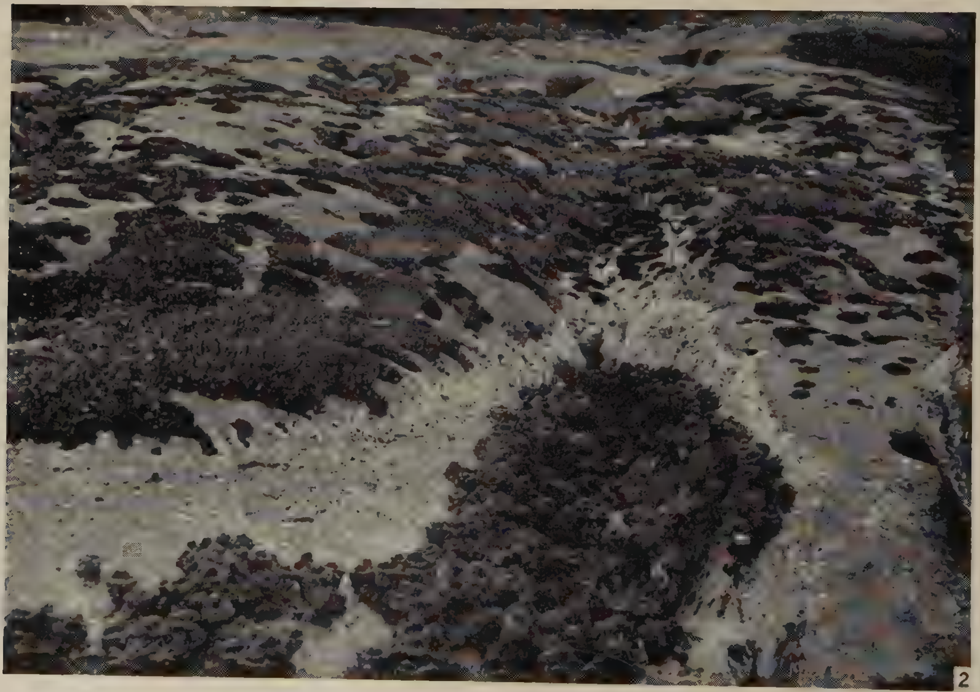
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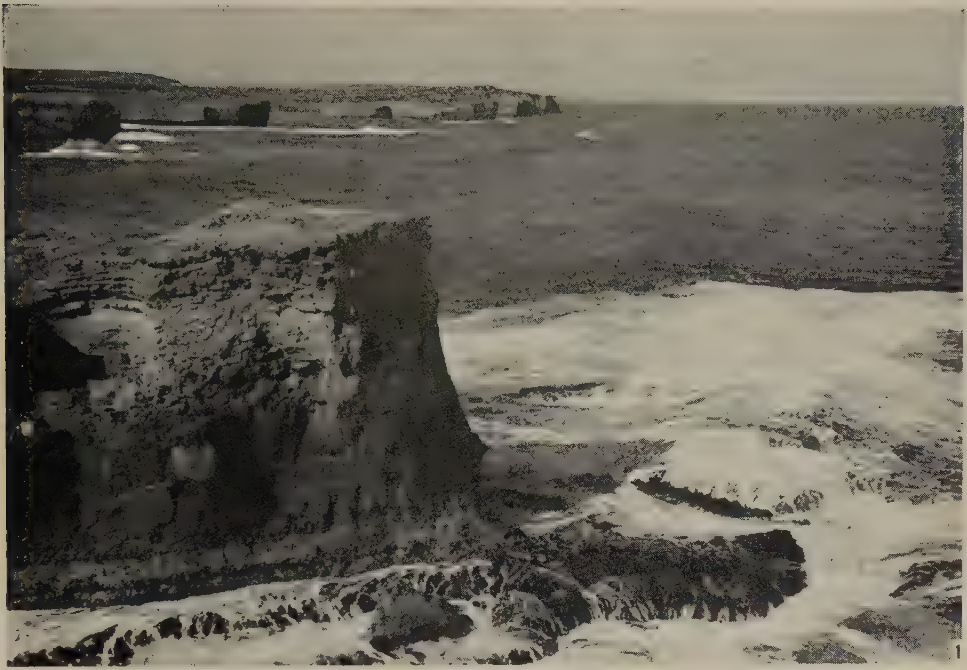
INTERTIDAL ZONATION OF VICTORIAN SHORES



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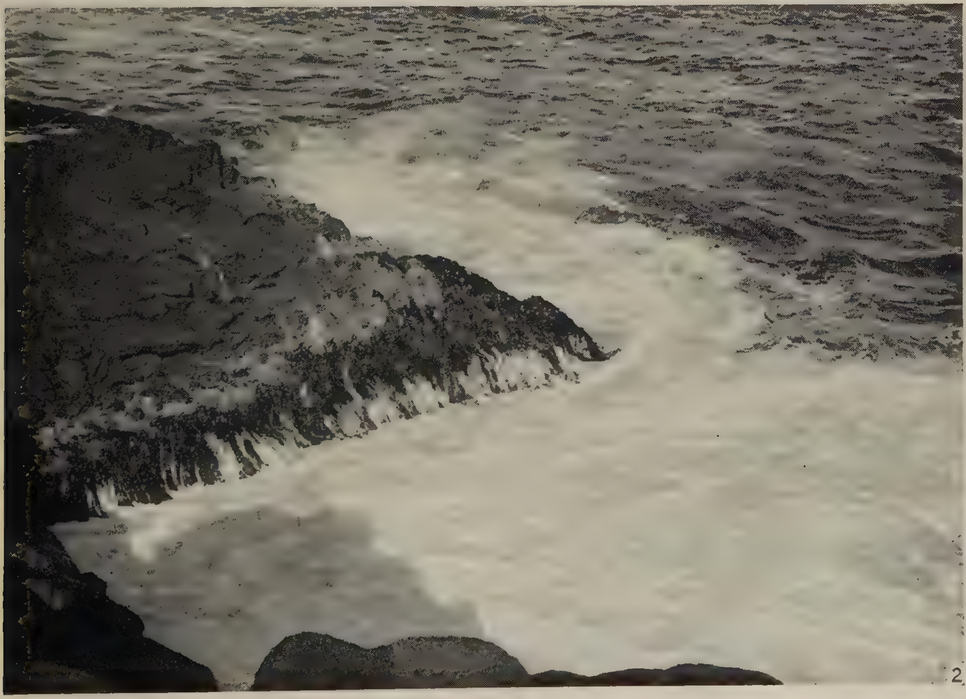

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WOMERSLEY, H. B. S. (1948).—The marine algae of Kangaroo Island. II. The Pennington Bay region. *Trans. Roy. Soc. S. Aust.* 72 (1): 143-66.

WOMERSLEY, H. B. S., and EDMONDS, S. J. (1952).—Marine coastal zonation in southern Australia in relation to a general scheme of classification. *J. Ecol.* 40 (1): 84-90.

EXPLANATION OF PLATES 1-6

With the exception of Plate 4, Figure 1, and Plate 6, Figure 2, photographs are by the authors

PLATE 1

Fig. 1.—Barnacles on the sloping red granite of Wilson's Promontory. The barnacle zone shows two distinct dark bands superimposed on the barnacles, the upper one being the mussel *Brachyodontes rostratus* and the lower, the alga *Splachnidium rugosum*.

Fig. 2.—The lowest intertidal zone at Wilson's Promontory—the top of the band of the giant fucoid *Sarcophycus potatorum* is just exposed (L.W.S.T.). Above this is a somewhat bare zone with a few *Pyura stolonifera*, then *Balanus nigrescens* (at feet of figure). Above this are the densely packed *Catophragmus polymerus*. At the extreme top left of the barnacles, a dark patch of *Splachnidium rugosum* may just be seen.

PLATE 2

Fig. 1.—Very distinct banding of *Pyura stolonifera* and the serpulid *Galeolaria caespitosa* (in its thin encrusting form) may be seen on the boulders at Norman Bay, Wilson's Promontory.

Fig. 2.—Extensive rock platform at Sorrento showing typical weathering of the dune limestone characteristic of so much of the southern coast of Australia.

PLATE 3

Fig. 1.—Dark band of *Lichina confinis* on rocks in the supra-littoral at Walkerville, Waratah Bay.

Fig. 2.—The alga *Ilea fascia* and the gastropod *Bembicium melanostoma* in the upper littoral at Lorne.

PLATE 4

Fig. 1.—The rock platform at Lorne—the mussel *Brachyodontes rostratus* dominates the mid-littoral. (Photo C. W. Brazenor.)

Fig. 2.—Zoning at Lorne. Looking shorewards along a depression on the rocks—the lowest band is of the ascidian *Pyura* above it a poorly developed *Galeolaria* band, then follows a well-developed band of the mussel *B. rostratus*. The few *Catophragmus* barnacles present may be seen as white specks on the mussels.

PLATE 5

Fig. 1.—The Port Campbell coast at low water. Note the vertical cliffs, and the narrow *Sarcophycus*-covered ledge at base of cliff in foreground. A scenic but inaccessible coast.

Fig. 2.—Very exposed point at Cape Bridgewater where constantly surging seas have pushed up the upper margins of the *Sarcophycus* and lithothamnion bands.

PLATE 6

Fig. 1.—*Brachyodontes* mussel band on a steeply sloping shore has a sharply defined upper limit at Nelson Bay. Barnacles are attached to the mussels in the upper two-thirds of the latter's vertical range.

Fig. 2.—A mixed algal community, mainly *Cystophora*, on a South Australian rock platform, but typical of *Cystophora* communities in western Victoria. (Photo H. B. Womersley.)

HETEROTROPHIC BACTERIA IN MARINE ENVIRONMENTS OF EASTERN AUSTRALIA

By E. J. F. Wood*

(*Manuscript received September* 18, 1952)

Summary

Bacteria in marine environments are almost entirely adsorbed on particles and their action is largely controlled by such adsorption. There is evidence of the existence of free enzymes or organic catalysts, possibly of bacterial origin. The extent of bacterial populations in certain marine environments is discussed and also the nature of the bacteria occurring in these environments. True anaerobic heterotrophs are almost, if not completely, absent. Marine bacteria are highly versatile in their reactions and variable in morphology, but do not differ sufficiently from soil and air forms to be regarded as distinct.

I. Introduction

Bacteria are of special interest in biological phenomena in that they always occur in Chapter I of the story, also that they initiate the metabiosis, i.e. the sequence of the organisms and of their impact on the cycle of matter. When an environment has to be converted for biological use, the bacteria usually have to be called in to perform the initial breakdown. This applies to many inorganic as well as organic components, e.g. the fixation of nitrogen, reduction and oxidation of sulphur, oxidation and reduction of iron, reduction of nitrate to nitrous oxide, nitrogen, and ammonia, etc. The large part of the breakdown of organic material is performed by the heterotrophs though it is by no means certain that they are always directly responsible. They may act by virtue of diffusible enzymes or more stable organic catalysts, which would account for the extent of organic breakdown in the sea in the absence of large numbers of bacteria therein. They also produce conditions which favour the action of autotrophs, e.g. the production of anaerobic conditions for the action of sulphate-reducing bacteria, or nutrilites.

The autotrophs, on the other hand, help to build up inorganic material into organic, working alongside the photosynthetic green cells to this end. They also produce changes of pH, redox potential, and other physicochemical conditions, which alter the balance of reversible reactions, such as the adsorption and desorption of phosphate, and possibly of bacteria themselves. Thus both autotrophs and heterotrophs are able to react directly on the physicochemical environment as well as to alter the chemical and biological environment. This is especially important in the sea, where there is a continuous aqueous phase for maximum activity, and where temperature changes are minimized.

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The present paper is concerned chiefly with the aerobic heterotrophs, about which more is known, and which attracted the interest of the writer in connection with their role in fish spoilage. Because spoilage bacteria were found on the surface of living fish (Wood 1940, 1950*a*; Stewart 1932), it was thought reasonable to suppose that these bacteria got there from the sea. The investigation was therefore extended to sea-water and marine and estuarine muds, and to submerged surfaces.

It is surprising that, despite a large number of studies of marine bacteria, no detailed attempt has so far been made to compare the flora of different marine environments. Possibly this is due to the chaotic nature of bacterial taxonomy. It is only when it is recognized that non-pathogenic bacteria are exceedingly variable in their characteristics, both morphologically and physiologically (Taylor 1942; Wood 1950*b*, 1952), that a comparison of bacteria in relation to their environment becomes possible.

II. METHODS USED IN THIS INVESTIGATION

Bacteriological sea-water samples were collected by ZoBell and Feltham's (1934) method where possible, but little if any difference in numbers or types was found in samples collected from Nansen water bottles which were used when glass samplers could not be, provided that the depth of collection did not exceed 50 m. and the sample was transferred to a glass container as soon as the bottle was brought to the surface. Mud samples were collected by using a glass-lined core sampler, and by brass core samplers and grabs, the mud being immediately and aseptically transferred to sterile containers. That grabs gave sufficiently aseptic samples is shown by the fact that many of the samples of bottom sands were sterile as regards heterotrophs. The taking of fish samples has been described (Wood 1940).

Sea-water and mud samples were plated on sea-water agar (ZoBell's medium 2216 with, at times, a little meat extract added), but for fish samples, tap water nutrient agar (S.A.B. formula) and fish agar (Wood 1940) were used, there being no significant difference in the growth of the fish flora on freshwater and sea-water agar. Where the bacteria could be made to grow on tap water media, these were used for differential tests which were based on the Manual of Methods issued by the Society of American Bacteriologists. Duplicate tap and sea-water media tests showed little variation for the tolerant organisms. Incubation was at 18° and 25°C. Dilutions were made by the standard technique using autoclaved sea-water as diluent.

The colonies used for classifying the flora were isolated from the greatest dilution of each sample showing viable organisms, so that only the predominant organisms were studied.

Various methods of making direct counts were studied, the standard ones used being those of Breed and Brew (1916) and Jones and Mollison

(1948). Haemacytometer cells were also used in certain cases. All methods suffered from the disabilities discussed by ZoBell (1946). He discusses the methods devised for direct counts of ocean water and comes to the conclusion that no really satisfactory method exists, as the duplicate counts deviate from the mean by 32.8-790 per cent. compared with 2.3-21.7 per cent. for plate counts. Centrifugation was inefficient for quantitative work in small populations, flocculation obscured many bacteria, and the best methods required a high initial concentration of organisms.

One of the chief difficulties, which has not been mentioned elsewhere, is the difficulty of separating microflagellates from bacteria. Some species of flagellates can be distinguished by the fact that the flagella stain by polychrome methylene blue, but the smaller flagellates (2-4 μ) are difficult to separate. An attempt has been made to use fluorescent microscopy, taking advantage of the fluorescence of chlorophyll with ultraviolet light and a yellow filter as suggested by Dr. Tchan (Linnean Fellow in Microbiology at Sydney) to count the flagellates, and the green fluorescence of living organisms with acridine orange to yield a total count. This method seems promising for estuarine water and the surface of muds, but does not solve the problem of concentrating the sea-water sufficiently for direct counts. A disadvantage is the fluorescence of certain non-living particles. The need to separate photosynthetic from heterotrophic organisms in the sea is obvious when one is concerned with productivity.

III. The Phenomenon of Adsorption

ZoBell has, in several of his papers, stressed the importance of adsorption in a marine environment. This phenomenon is of paramount importance, not only in its effect on plate and direct counts of bacteria, but in determining the course of chemical and biological reactions. It has been found in this laboratory that muds containing a large silt fraction are far more difficult to oxidize than muds with a small silt fraction, both hydrogen ion concentration and redox potential being far more stable when the silt fraction is high. In the culture of autotrophic sulphate reducers, reduction is almost entirely confined to surfaces, as shown by film formation on the walls of the vessel, and by inoculation experiments. The latter usually failed unless the surfaces were scraped to provide an inoculum.

Studies were made by the writer on the adsorptive capacity of muds for bacteria. Rubentschik, Roisin, and Bieljanski (1936) found that bacteria in salt lakes are adsorbed on mud particles which are positively charged, the living bacteria being negatively charged. They found that the viability of bacteria is not adversely affected by adsorption, and suggest that, in certain cases, the muds may adsorb metabolic products. Desorption also occurs, and adsorption and desorption may occur simultaneously. These writers found an adsorption of 99.2 per cent. at an optimum concentration of 10×10^6 bacteria in 5 g. of mud.

The writer adsorbed bacterial suspensions on sterile estuarine muds of measured particle size obtained by shaking and sedimentation. The bacteria were gently shaken with the mud for ½ hr., centrifuged at constant speed to settle the mud particles, the supernatant plated, and bacteria counted. It was found by microscopic determination that optimum adsorption occurred on particles of 1-2 μ diameter (up to 99.8 per cent. of bacteria adsorbed), but good adsorption occurred on particles between 20 and 5 μ. Also, there appears to be, as Rubentschik stated, an optimum con-

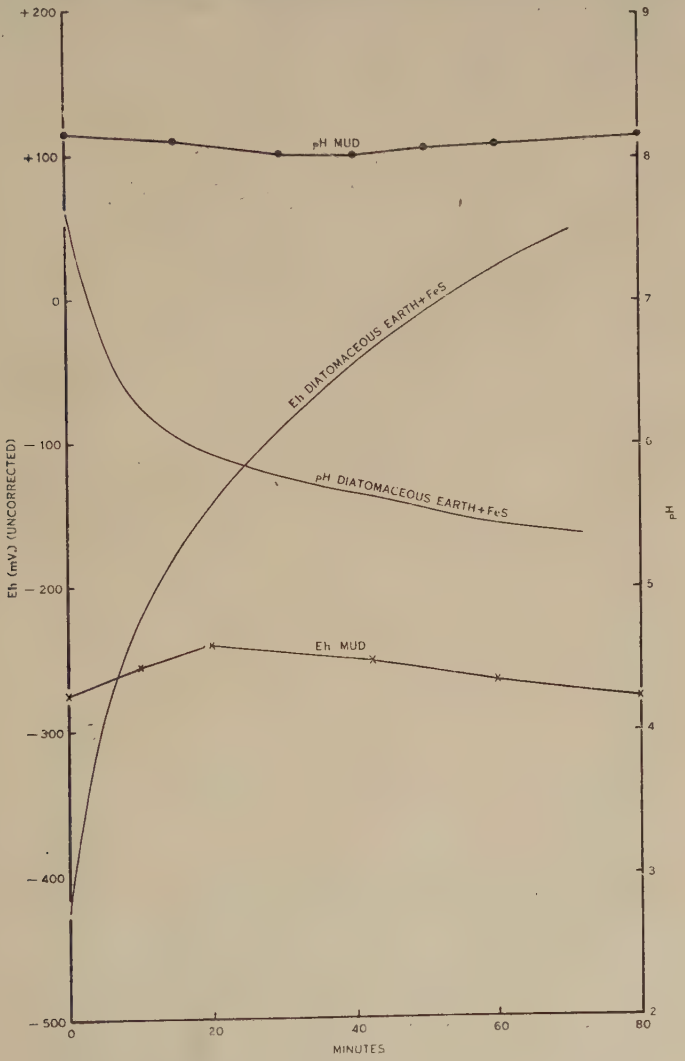

Fig. 1.—Poising of natural silt fraction of a natural sulphide mud compared with an artificial mud with diatomaceous earth and N/10 ferrous sulphide.

centration of bacteria for maximum adsorption. Adsorption was higher (99.8 per cent.) in concentrations of 5 × 10^5 bacteria per ml. than with 4 × 10^4 (95.9 per cent.) or 5 × 10^6 (91.2 per cent.) (Appendix I).

Adsorption also occurred on washed diatomaceous earth, but not to the same extent as on muds. The difference may be due to the buffering and poising capacity of the organic matter in the latter (Fig. 1) or to surface charge, or possibly to both.

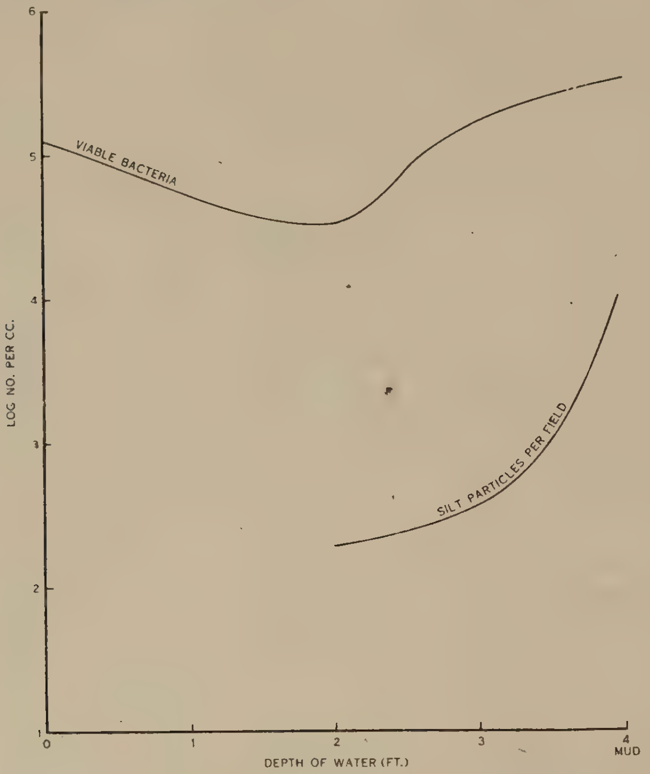

Fig. 2.—Log. viable bacteria per cc. and number of silt particles (25 μ or less) per microscopic field in the water of the tidal zone from the surface to 4 ft. Note the increased population at the surface (surface film effect) and in the zone above the mud due probably to turbulence (hydrographic evidence supports this theory). The figures shown are the means of a number of counts at Shell Point, Botany Bay. Similar tests at Maianbar, Port Hacking, gave curves of similar shape.

It is probable that, in shallow water, the adsorptive ability of muds reduces the bacterial population of the overlying waters in tidal areas where there is some turbulence. At any rate, the bacterial population is greatest just above the mud in the water containing most silt particles (Fig. 2).

IV. Bacterial Numbers in East Australian Waters

(a) *Sea-water*

Sea-water samples have been collected from four stations between Lat. 34° and 37°S. at monthly intervals since 1948. They were taken at depths 10 m. apart from 0 to 50 m., plated on sea-water agar, and counts and isolations of the dominants made. Plate counts averaged about 100 bacteria per ml. of sea-water, but ranged from 4 to 500 per ml. The counts from April to August or September are significantly higher than those from October to March, ranging from 4 to 50 in the summer and from 50 to 250 in the winter (Fig. 3). ZoBell and Feltham (1934) found a maximum count in July-August corresponding with the period of highest water temperature. The temperature range was roughly from 12 to 20°C. while in east Australian waters the range is between 14 and 25°C. There would appear to be an inverse relationship between bacterial populations and temperature in Australian waters, but the coast of southern New South Wales has a winter rainfall, and there is frequently an onshore movement of the East Australian current resulting in an increased population of diatoms and dinoflagellates. It is impossible at present to evaluate the effect of these factors on the bacterial population on this coast. Only on few occasions was a bacterial count of more than 1000 per ml. obtained from sea-water, notably from off Botany Bay on 23.v.49, accompanied by a *Chaetoceras* peak, and in July 1949 all along the coast following heavy rain and the flooding of the rivers. A summer minimum and winter maximum was recorded from Lake Zürich by Pfenniger (1902). In the summer,

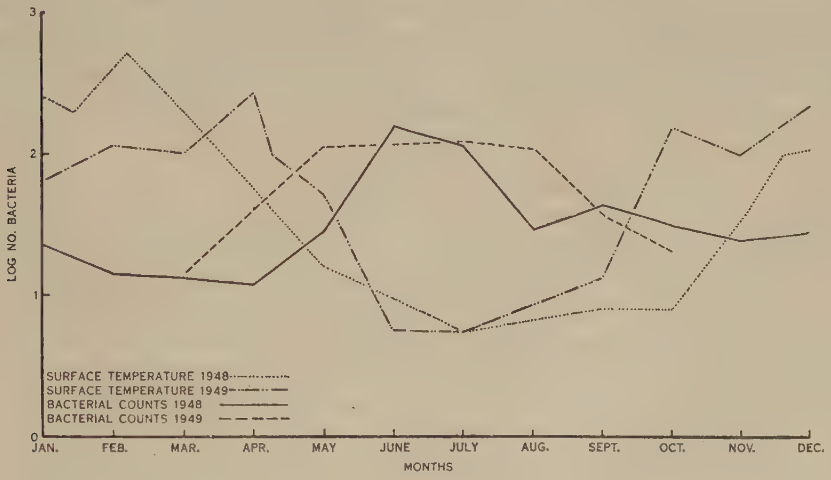

Fig. 3.—Bacterial counts of surface sea-water off Jibbon Cape, 1948 and March-October 1949, showing winter peak. Surface temperatures for the same period are also shown. The inverse correlation may well be apparent rather than real, direct influences being winter rainfall and current movements.

too, the number of bacteria changed but little from 0 to 50 m. depth, but from April to October the greatest number occurred between 20 and 40 m. In almost every instance the minimum number occurred at 10-20 m. (Fig. 4). ZoBell and Feltham (1934), using plate counts, found that the highest number of bacteria occurred between 20 and 50 m. below the surface. Unfortunately the author's observations did not go below 50 m. but the general picture seems the same. The number of bacteria at the surface was usually greater than that at 10-20 m. ZoBell and Feltham (1934), using plate counts, found between 43 and 410 bacteria per ml. 10 miles west of La Jolla, California, so that the numbers found in Australian waters are comparable.

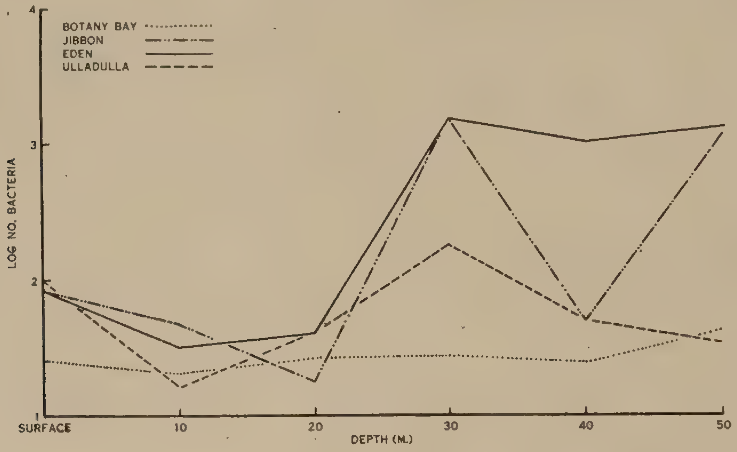

Fig. 4.—Relationships between population and depth, 10 miles offshore, at four stations off eastern Australia (Lat. 34°-37°S.).

In order to find a relationship between direct and plate counts of bacteria in sea-water, the author carried out a number of tests in Botany Bay where the counts were high enough for Breed and Brew's (1916) method and Jones and Mollison's (1948) method to be used. It was found by comparing plate and direct counts of sea-water suspensions of increasing dilutions of cultures, that the discrepancy decreased as the number of bacteria fell away (Appendix II). Microscopic examination of the silt particles by phase contrast showed that the distribution of bacteria thereon became more even as the number of bacteria per available particle decreased, so that the discrepancy between plate counts and total population is likely to be much less in the open sea than in estuaries or muds. Nearly all the bacteria in the direct counts were adsorbed on the particles. This means that plate counts of bacteria in the sea represent the actual state of affairs more truly than plate counts of muds or estuarine waters.

It is recognized that plate counts assess only the viable aerobic heterotrophs, but there is no evidence of the presence of strict anaerobes

(Appendix 3) nor are there the conditions requisite for the existence of autotrophs in the open sea, except perhaps in the vicinity of plankton swarms. This points to the validity of the assumption that plate counts in the open sea are of the same order as the total number present, an assumption that is false for bottom deposits. It is very doubtful whether it would apply to counts in plankton swarms owing to adsorption and consequent clumping.

There has been practically no work done on the bacteriology of plankton swarms, but the author's experience of the adaptability or variability of marine forms would suggest the functions of bacteria in this milieu may be as diverse as in bottom deposits.

(*b*) *Muds*

It is very difficult to assess with any degree of accuracy the bacterial population of muds. Viable counts made by the poured plate technique fall below the direct microscopic count by 100-10,000 times, and the author has not found any constant relationship between the two (Fig. 5). This is understandable because a large and varying part of the flora is autotrophic or facultatively autotrophic, so that even a summation of counts to include all the recognized processes is useless. Further, as the author has shown (see above) the number of bacteria adsorbed depends on several factors.

Total counts do not allow one to distinguish between the bacteria and the colourless flagellates which abound in this milieu. Estimations by chemical means, such as assessment of the albuminoid protein, have the same disadvantage. Because of the difficulty of finding a satisfactory method of direct counting, the results below refer to plate counts, which are used to give relative numbers only. Bacteriologists will recognize their limitations.

The muds of the continental shelf off Port Hacking have a heterotrophic bacterial population between 1×10^5 and 3×10^6 per gram by plate counts made over some 2 years, but the sands were found to be sterile of these organisms. Waksman and Hotchkiss (1938) showed that sandy bottoms consume little oxygen, and Waksman and Vartiovaara (1938) suggest that muds adsorb bacteria whereas sand does not (no doubt on account of charge and particle size). ZoBell (1946) also records that the sands of the continental shelf contain few bacteria, the population being related inversely to particle size, which is, in turn, related to nitrogen and organic content, and the adsorption phenomena involved. Core samples have not been taken owing to lack of a satisfactory sampler.

Bacterial plate counts of estuarine muds in the oyster-growing regions of Botany Bay range from 8×10^4 to 2.5×10^7 per cc., having their maximum at the region of maximum pH. This fits the positive charge theory of adsorption. Examination of weekly samples from depths of 0-4 ft. show little diminution of the bacterial count with depth in the intertidal zone, suggesting vertical water movement.

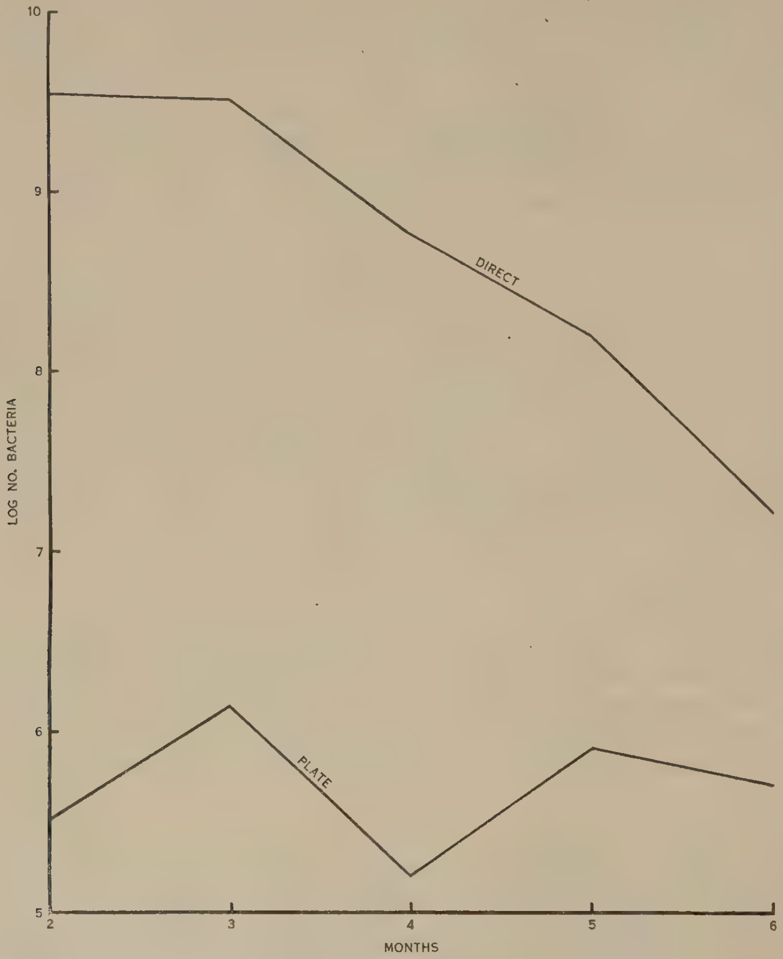

Fig. 5.—Mean direct and plate counts of 13 mud samples at Shell Point, Botany Bay, over 5 months.

The weekly plate counts showed, over 6 months in 1952, a random variation ranging at the surface of the mud from 4 × 10^3 to 3 × 10^7. In monthly samples taken in 1949, the plate counts did not show a definite pattern (Fig. 5) but the direct counts showed a steady diminution from February to June.

It was found also that, when 13 samples were taken weekly from the same region, the variation between samples was far less than the random variation between successive samples.

It would seem from this evidence that only direct counts are of value in following population trends. This suggests that the heterotrophic population varies rapidly with changing conditions of tide, weather, etc., and is of little value to the investigation until the controlling factors are known.

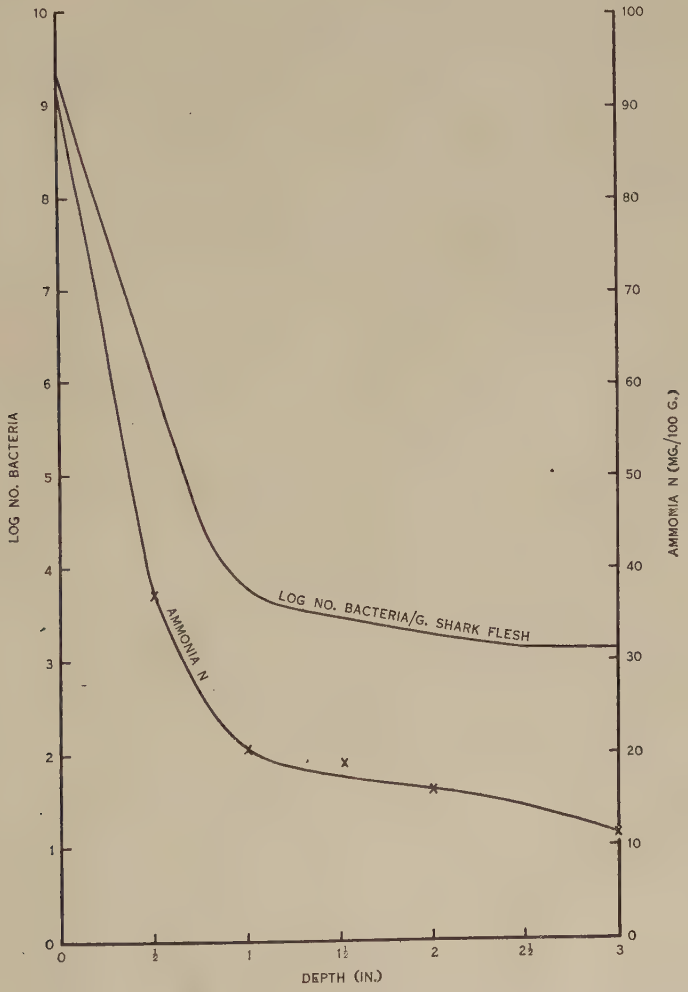

Fig. 6.—Curves showing decrease of bacterial populations and of ammonia with depth from a cut surface in shark flesh.

(c) *Submerged Surfaces*

For submerged surfaces, the author has found that, in Australian waters, even in Sydney Harbour with its high content of organic matter and very high fouling population, bacteria did not form a film on glass slides even after 3-7 days (Wood 1950*d*). This may be due to the activity of protozoa which the writer has observed on these slides and which certainly consume bacteria, as can be seen by observation.

(*d*) *Fish*

Fish spoilage was shown (Wood 1940, 1950*a*) to be very largely a surface phenomenon, the large majority of bacteria occurring on the cut surfaces, while the numbers decrease very rapidly with depth. With shark taken from Melbourne fish market and in good marketable condition, plate counts from the scraped surface flesh were of the order of 10^9 bacteria per gram on shark agar, while at 0.5 cm. depth they had fallen to 10^7 and at 2.5 cm. to 10^4 per gram (Fig. 6). It was also found with spoilage bacteria that the rate of reproduction and of urea decomposition decreased rapidly with increased carbon dioxide tension, no ammonia being produced from Ashworth's urea agar at 50 per cent. O_2 tension or less in eight cultures, though all of them subsequently produced ammonia in the same tubes in air. The curves in this case followed those in Figure 6 for shark flesh.

One other interesting point in this connexion is that the gut of fish which have not been feeding is sterile, i.e. contains neither aerobic nor anaerobic bacteria (Wood 1940).

V. CERTAIN CHARACTERISTICS OF THE MARINE BACTERIAL FLORA

ZoBell (1946) in his classic monograph on marine microbiology lists the genera of bacteria recorded as having been found in the sea. He naturally uses Bergey's classification (Breed, Murray, and Hitchins 1946) which was generally accepted at the time. It is only recently that a revolt has occurred against Bergey's system, which began as a praiseworthy attempt to systematize bacterial classification but has lost most of its usefulness on account of its rigidity. Kluyver, Rahn, van Niel, and others, including the author (Wood 1950*b*) have shown that the Linnean species concept cannot be applied to bacteria, and now that the study of general, as opposed to medical, bacteriology has shown the fluidity of bacterial reactions, the idea of a bacterial species as subjective rather than an objective entity is gaining acceptance in Britain, Europe, America, and Australia. This clears the ground for an ecological appreciation of terrestrial and marine environments that was impossible before.

Taylor (1942) reached the same conclusion as the author (Wood 1950*b*, 1952) as regards the classification of soil and freshwater bacteria, namely that the usual biochemical tests are useless in the classification of such forms. He states: "It appears certain that the majority of bacteria found in water cannot be adequately classified by the old biochemical tests," and in view of similar findings by workers with soil bacteria, it seems that this applies to a large proportion of all bacteria found in nature, except those which develop at body temperature. Taylor and Lochhead (1937) came to the conclusion that soil organisms in general, being physiologically unstable, show adaptation to changing conditions, and are thus difficult to classify on a physiological basis. Conn, Wolfe, and Ford (1940) have endorsed this view and consider that "progress in classification may be made more adequately by a study of gram reaction, type of flagellation, and tendency to show true or false branching or irregularities in the shape of cells. Such points should give a basis for classification, but it is desirable that the characteristic function of the organisms should be taken into consideration, for the role of most of the indigenous bacteria in soil or in water still remains to be solved."

Considering chiefly the soil and water forms Wood (1950*b*) concluded that "The usual biochemical tests have not, in the organisms I have investigated, stood up to the test. They seem to vary too much within a given strain, and cannot be correlated with one another or worked out on a statistical basis." In addition, these characters are alterable by a single mutation, and such alterations must be very frequent in organisms with such a rapid rate of multiplication.

The question of adaptability versus variability is interesting, and there seems to be evidence (that of the possibility of "training" bacterial strains) that such trained strains are in fact selected variants of clones with a wide variability pattern. Such selected variants would not necessarily have the wide range of variation of the parent and would appear to be a new physiological strain. The more generally accepted theory that some strains are more adaptable than others cannot be ruled out by the author's personal experience. Organisms which grow with equal readiness in sea-water and fresh water or under aerobic or anerobic conditions may be adaptable without a change in the hereditary characters of the cell, or may be variable, with a wide and rapid variation rate.

Taylor (1942) considers also that "the only characters which appeared to be of real value were the colours produced on solid media and the liquefaction of gelatine" although "it is probable that colour may be lost, gained or modified but, in general, it was found that cultures of the same colour, shade and type were replicates." The author (1952) came to the same conclusion as regards pigmentation in the micrococci and the corynebacteria (Wood 1950*a*), but found that gelatine liquefaction was less reliable.

While ZoBell (1946) recognized the versatility of marine bacteria, stating, "It is believed that there are bacteria in the sea which are capable of attacking nearly any kind of organic substrate, and many inorganic compounds are altered by the activities of marine microorganisms," he did not stress the fact that the same species and even the same strains may alter their activities. He then differed from the present author in believing that there is a specific marine bacterial flora. This difference of opinion is explained by a marked change of viewpoint since 1946 by bacteriologists in general and by a different approach to the species concept for bacteria rather than by opposing evidence. ZoBell and Upham (1944) described

60 new species of marine bacteria which they regard as a part of this specialized marine flora. They have based their conclusion mainly on the difficulty they found in growing freshly isolated marine bacteria on freshwater media, and on the bactericidal effect of sea-water on freshwater and soil forms. In the author's experience, based, it is true, on the flora of the continental shelf and of estuarine environments, many of the bacteria isolated grew nearly as well on freshwater as on sea-water agar just after isolation, and the majority did so after a few subcultures or after strain selection by various concentrations of sodium chloride, although at the few truly oceanic stations sampled, counts on sea-water agar were about four times those on freshwater agar. The majority of soil organisms isolated by the author from Cronulla soils had a wide salt tolerance, and grew reasonably well on sea-water agar. These included the genera *Staphylococcus, Mycoplana, Corynebacterium,* and *Bacillus.* It was found also that bacteria from marine sources had as wide a temperature tolerance as those from soil, most of those isolated at 18 or 25°C. growing at 37°C., and a few even at 45°C. The bacterial cultures were tested by incubating them for 14 days at 37 or 45°C. and subculturing to sea-water nutrient agar and peptone water after 7 and 14 days. Failure to grow on subculture was regarded as a criterion of death. Of 142 cultures tested, 42 per cent. were killed at 37°C. (nearly all cultures of *Corynebacterium* from shark) 24 per cent. at 37°C., 17 per cent. at 45°C., while 15 per cent. survived this temperature. All genera showed heat-tolerant strains. The tolerance of high temperature by marine bacteria in this latitude (34°S.) compared with those isolated by ZoBell, Waksman, and others is no doubt related to the fact that summer water temperatures are of the order of 24-26°C., and in shallow water, or at times under certain conditions in deeper water, the water temperature may reach 30°C. or higher. It was found that estuarine sulphate reducers react more rapidly at 30°C. than at 25 or 18°C., and that they are still active at 55°C. Iron bacteria and the purple and green sulphide-oxidizing bacteria from the same source are also active at 30°C.

Studies on the bactericidal effect of sea-water were made (Appendix IV). It was also found that, in accordance with Waksman and Hotchkiss' results (1938), sea-water is bactericidal to both marine and soil bacteria in culture, and there was no significant difference. Exposure of soil and marine bacterial cultures (10 of each) to freshly collected sea-water for ½ hr. reduced the count to 0.2 per cent. of the control suspended in artificial sea-water. Sea-water filtered through a bacterial sintered glass filter, in contact with the cultures for 2 hr., and autoclaved sea-water showed no bactericidal properties (Appendix IV). Waksman and Hotchkiss concluded that the bactericidal agent does not interfere with the decomposition of organic matter measured by oxygen consumption. The bactericidal property of sea-water could hardly be due to antagonism or to the production of toxins by marine bacteria already in the water, owing to the small numbers present. Moreover, either of these factors would prevent the rapid increase of population in sea-water on storage reported by ZoBell (1940) and other workers. One cannot postulate that toxins are adsorbed on the walls of the vessel in such experiments, as we know that bacteria are adsorbed thereon and remain viable (ZoBell 1946). Apparently, bacteria living in the environment are immune to the bactericidal property, and can increase on storage or in a plankton swarm, yet these same bacteria lose their immunity on subculture on artificial media and re-exposure to sea-water. The author has observed at times clear plaques in poured plates inoculated with sea-water, suggesting that the bactericidal property might be due to a bacteriophage, as has previously been suggested by Fernand, Sempe, and Chavanne (1925). Filtration through sintered glass could well adsorb the phage, and autoclaving would destroy it. Sea-water bacteria grown on artificial media for some time could be expected to lose their resistance through the development of non-resistant strains, with the result that they would be killed off by subsequent exposure to sea-water.

Taylor (1948) states that, in Lake Windermere, bacteria entering the lake from rivers disappear more rapidly than can be explained by dilution, so the bactericidal effect is not confined to sea-water. Once again, bacteriophage would explain the phenomenon, and would also explain Waksman and Hotchkiss' observations on the decomposition of organic matter. However this may be, since the bactericidal property is common to fresh and sea-water environments, it cannot be used as an argument in favour of a distinct marine bacterial flora.

Sea-water is far more bactericidal to coliform bacteria than fresh water, as the author found in his studies of Melbourne water supplies and sewage outfalls. This is probably due to increased electrolytes in sea-water and intolerance of the specialized coliform bacteria thereto, or to a change in the ionic balance of the milieu. The presence of coliform bacteria in rivers and in soil depends on animal pollution, i.e. is really adventitious, and cannot be used to differentiate fluviatile and terrestrial from marine biospheres. Recently, extremely salt-tolerant coliform bacteria have been reported.

The predominance of Gram-negative forms in the sea (Table 1; Fig. 7) and Gram-positive forms in the soil, and the relative absence of true anaerobes in the sea is evidence in favour of a marine flora, but not necessarily a specialized one. The author has found that the predominant forms in the sea resemble those described by Topping (1937), Jensen (1934), Gray and Thornton (1928), and Taylor and Lockhead (1937), i.e. Gram-negative and Gram-positive pleomorphic forms and cocci, though the ratio is quite different. Acid-fast bacteria were found by the author to be rare to absent in water with a salt content of more than 2.5 per cent., probably owing to the effect of electrolytes on the envelope of the bacteria. Strains of *Actinomyces* isolated from the sea are usually not acid-fast.

One would expect that bacteria living in the sea would have a greater salt tolerance than soil forms as a result of the adaptation of strains to or variation with the environment, just as one would expect soil forms to have a greater resistance to desiccation than marine forms. The association of motility with marine forms remarked upon by ZoBell is a natural one, but, once again, motile forms are characteristic of fresh water also. It is no doubt significant that, whereas Topping found occasional motile corynebacteria in soil, the author has found them quite common in marine environments (Section VI). The finding of *Sporosarcina ureae* 10 miles east of Port Hacking (Wood 1946) suggests a relationship between sea-water and land floras.

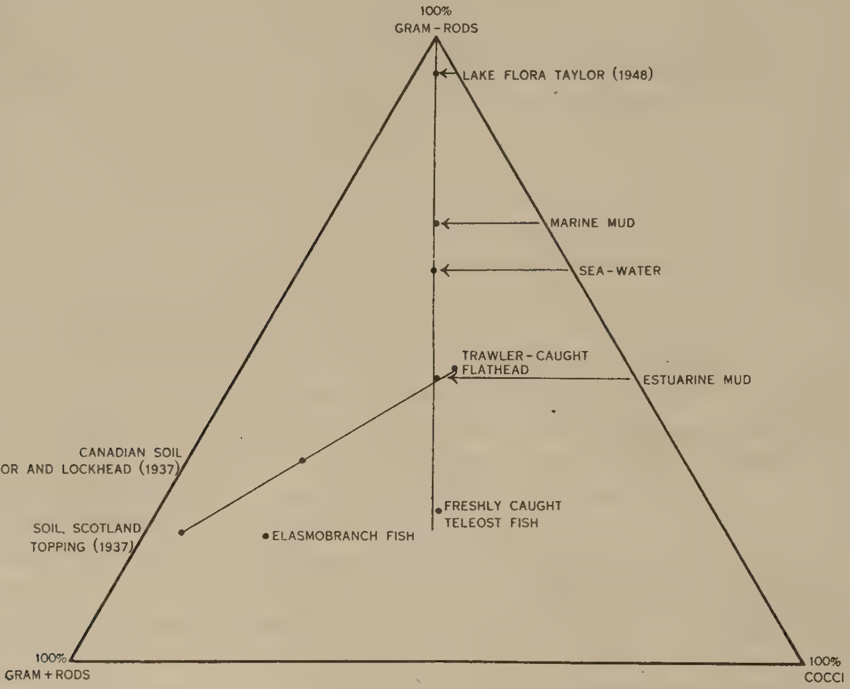

Fig. 7.—Diagram showing proportions of Gram-negative and Gram-positive rods and cocci in certain terrestrial and marine environments.

Functionally too it is difficult to separate marine and terrestrial bacteria. The *Pseudomonas* species of both environments are chiefly proteolytic, but ferment glucose and frequently reduce nitrates to nitrogen, the bacilli are both proteolytic and saccharolytic, and the cocci mainly saccharolytic. There is a difference in that galactose, mannitol, and laevulose are fermented by marine forms more frequently than by terrestrial ones which most commonly attack glucose, but on the other hand, there are many marine bacteria which decompose starch, a relatively rare substance in the sea, while soil bacteria and even Basidiomycetes sometimes liquefy agar, which is still rarer in soil.

The autotrophic forms occurring in estuarine muds include all those commonly found in soils, except for the root-nodule bacteria, and perhaps a few other species. *Azotobacter* is recorded in the literature, and has been found by the author in muds at pH 8.1 and a salinity of 2.5-3 per cent. at Shell Point, Botany Bay, on several occasions, and isolated on Winogradsky's medium (Winogradsky 1949). Sulphate reducers are abundant, and so are the sulphur bacteria, including the purples, greens, and Beggiatoas, the iron bacteria, and so on. Sulphate reducers occur even in the coarse cream sands of the Sydney beaches, and have been cultivated therefrom in sea-water sand medium and in Starkey and Wight's medium (Starkey and Wight 1943) with anaerobiosis.

The marine flora would, on the evidence, appear to be a distinct flora in the same way that river water contains a distinct flora from soil; the ratio of genera to one another is different, and there is also a species selectivity brought about by different biocoenoses, while some species are absent in certain biocoenoses. The differences, however, are of degree rather than of kind (Fig. 7).

A study of the literature of marine bacteriology shows that different workers have found a very different flora. Certes (1884) found spore-formers in sea-water and bottom deposits, Fischer (1894) found helicoidal spirilla and pleomorphic forms, with no streptococci or sarcinae, most of the bacteria being motile and Gram-negative: some bacteria showed polar bodies. Russell (1891) considered that mud and sea-water had different floras. He isolated several species of *Bacillus*, including *B. sphaericus*, *B. mycoides*, and *B. cereus*, all of which have been met with in the present investigation. He also found a number of vibrios and spirilla and records that pigment production and pleomorphism were common. Some of the forms would not grow in fresh water. Otto and Neumann (1904) found Gram-negative rods and vibrios, as did Hesse (1914) whose cultures grew as well in fresh water as in salt. Issatchenko (1914) isolated a number of rods and also cocci.

The differences observed are no doubt partly due to technique but largely reflect the differences in different parts of the world, and in different seasons. As an instance of this, *Bacillus* was common in Botany Bay muds in 1948, about a tenth as abundant in 1949, and one-twentieth in 1950, while micrococci were far more abundant in 1949 than in other years, both in estuarine muds and in sea-water. Up to 1949, cocci were rare in sea-water, and were regarded by the author as derived from the land or from fresh water, but, in 1949, they were both abundant and widely distributed, in fact at times they were the dominants, even 10 miles offshore in the region affected by the oceanic east Australian current.

(*a*) *Morphological Characters*

Pleomorphism has been remarked upon by Fischer (1894), Russell (1891), and ZoBell (1946). Although Winogradsky (1949) considers it an artefact due to growing bacteria on unsuitable media, the evidence is in favour of the existence in nature of this phenomenon. It occurs in sulphate reducers grown on organic and inorganic media, and in pure cultures of these organisms in a sterile mud-seaweed-sea-water system, as has been observed in this laboratory. The writer has also observed a range of forms on a slide which has been immersed in the sea for several hours and then examined by phase contrast, and the same range in pure cultures isolated from the same slide. That these are not degenerate forms is shown by the fact that they appear during the logarithmic growth phase.

Pleomorphism is characteristic of the Australian marine bacterial flora, both in the Gram-negative and Gram-positive rods. This phenomenon is also common in soils (Topping 1937; Jensen 1934; Gray and Thornton 1928). These authors have recorded it in *Corynebacterium, Mycoplana, Actinomyces,* etc., so it cannot be regarded as defining the marine flora. As ZoBell says, nearly all the rods are motile by means of polar flagella, which are difficult to stain. One character which has received little comment is the presence of granules, the "polar bodies" of Fischer. These are very common in a majority of the cultures examined in the genera *Mycoplana, Corynebacterium,* and *Bacillus.* The *Sarcina* strains are often intensely Gram-positive, rarely Gram-negative. Branching forms occur, but are not abundant in *Mycoplana* and *Corynebacterium.* Morphological characters were studied by frequent microscopic examination of agar slide cultures, fixing colony location by the stage vernier.

(*b*) *Physiological Characters*

Marine bacteria, like soil bacteria, are extremely versatile. The writer has found that, even in single cell culture, strains frequently arise which differ from the parent culture in their biochemical reactions. The observed differences are usually a loss of function, e.g. sugar fermentation, agar liquefaction, etc., but at times the organism may show an additional reaction, e.g. nitrate reduction. This does not necessarily mean a gain in enzyme systems, but that conditions are such that the strain with the enzymes under test strongly developed predominates in the culture. Such a selection of strains can frequently be made by rapid subculture in the medium to be attacked, and selection of the most active culture or colony for each successive subculture. Furthermore, strains having a random pattern of biochemical reactions may be isolated from a given subtrate, e.g. shark flesh. Such strains were found to vary in respect to proteolysis, urea decomposition, carbohydrate breakdown, temperature tolerance, etc., precluding separation by biochemical tests into species or even races. Many agar digesters differed from each other in their other biochemical reactions yet were identical with strains which did not attack agar except for the one property of agar digestion. In many instances agar digestion was only observed when the cultures were grown on media poor in nutrients, i.e. the property was masked in the usual agar media such as nutrient agar but appeared on plates of washed agar or 1-5 per cent. soil extract sea-water agar. Different agars accentuated or depressed fluorescence of *Pseudomonas*, and of *Corynebacterium erythrogenes*, e.g. Japanese agar media gave good fluorescence whereas *Gracilaria* agar did not, the other ingredients being identical. The author has recently found some evidence that some Gram-negative pleomorphic aerobes can reduce sulphates, though this requires confirmation.

Because of these results, the writer considers that the versatility of marine bacteria is due to rapid variation under the impact of or adaptation to environment on the part of a few species rather than to the presence of a number of species with rigidly marked properties.

(*c*) *Nitrogenous Material*

ZoBell considers that "as a group, marine bacteria are more weakly saccharolytic and probably more strongly proteolytic than either soil or fresh-water bacteria." Taylor (1942) found that lake bacteria showed weak physiological activity, especially as regards litmus milk and glucose, but that many of them (50 per cent. from Rydal Water and about 40 per cent. from Windermere) liquefied gelatin. The author found that approximately 50 per cent. of bacteria from Victorian reservoirs liquefied gelatin. Among the marine strains studied by the author, proteolysis, as shown by lysis of fish protein (Wood 1940), liquefaction of gelatin, and peptonization of milk was observed in 33-50 per cent. of the strains tested (Wood 1940, 1950, 1952) but liquefaction of gelatin and peptonization of milk were nearly always slow. Reactions in milk were found to vary in a series of cultures from the same single cell strain. Urea was decomposed by a majority of strains (Wood 1950*a*) and amino acids were broken down by about 30 per cent. Strains isolated from fish were, on the whole, more proteolytic than those from sea-water and muds, as might be expected. Indol is very rarely produced from tryptophane, as previously reported (Wood 1940) and amply confirmed subsequently, less than a dozen indol-positive cultures being encountered among nearly 3000. Many strains reduced nitrate to nitrite, but few reduced it to nitrogen. Nitrate reduction was very inconstant (Appendix 5), even in separate colonies of the same strain; more recent work by the writer confirms earlier statements made (Wood 1940, 1950, 1952). *Azotobacter* and purple bacteria (Lindstrom, Lewis, and Pinsky 1951) reduce atmospheric nitrogen to ammonia.

(*d*) *Carbohydrate Fermentation*

Taylor (1942) comments on the failure of most of his freshwater strains to ferment carbohydrates. Apart from the coliform organisms this also characterized the Victorian rivers examined by the author. In the

Australian marine bacteria, starch was hydrolysed and two or more sugars fermented by 45 per cent. of the strains tested. This included isolates from fish, sea-water, and muds, the percentage of saccharolytic strains being approximately the same from each source. Glucose, maltose, galactose, saccharose, and mannitol were the carbohydrates most frequently attacked, pentosans being attacked much less frequently. It is significant that galactose and mannitol were more frequently fermented than is usually recorded for terrestrial bacteria (see for instance Wood 1952), as agar is a galactan and mannitol is a component of the brown algae. Cellulose digestion was surprisingly rare in cultures isolated on agar, though cellulose digesters may be readily demonstrated in estuarine waters by appropriate means, and appear to play an important part in providing the low oxygen tension required by the sulphate-reducing bacteria in estuarine muds.

(*e*) *Agar Digestion*

Agar digesters are common in sea-water and mud at times, but none was isolated from fish. Taylor records none from British lakes, though they do occur in soil. Agar digesters were found to form 2-5 per cent. of the sea-water flora and 1-2 per cent. of the mud flora. However, these figures are probably low, as it was not realized until late in the research that agar digestion rarely occurs if the nutrients in the medium are high (see above).

(*f*) *Alginic Acid*

Alginic acid was attacked by isolates from *Ecklonia radiata*. Other marine bacteria were not tested for this property. Thjøtta and Kåss (1945) found that 6 per cent. of bacteria from sea-water and 4.5 per cent. from soil attacked alginates. The organisms were pleomorphic, irregularly staining forms resembling those placed by the present author in the genus *Mycoplana*.

(*g*) *Activity of Autotrophic Bacteria*

Autotrophic bacterial transformations are as marked in marine muds as they are on land, and are possibly even more rapid.

(*h*) *Pigmentation*

Taylor (1942) records between 21 and 54 per cent. of coloured colonies, mainly yellow, in lake water in Britain. In Victorian river waters the pigmented strains were mainly green-fluorescent *Pseudomonas*. ZoBell (1946) records that 69.4 per cent. of bacteria from sea-water or mud produced pigment. The writer found that the great majority of bacteria from muds (85 per cent.) and sea-water (87 per cent.) are non-pigmented but that those isolated from fish show a preponderance of coloured forms (57 per cent. for teleosts and 80 per cent. for elasmobranchs), mainly yellow. The pigmented strains from marine muds were pink to red. The red-fluorescent *Corynebacterium erythrogenes* appeared in 2.5 per cent. of cultures from teleosts and 9.3 per cent. from elasmobranchs, but did not occur in sea-water or mud. Fluorescent strains of *Pseudomonas* were common in teleosts (16 per cent.), less common in elasmobranchs (11 per cent.), and rare to absent (less than 1 per cent.) in the sea and in muds. These strains are exceedingly common in Australian rivers. Orange and pink strains of a *Bacillus* morphologically resembling *B. subtilis* were sometimes numerous in estuarine muds. These forms do not seem to have been recorded previously.

(*i*) *Luminescent Bacteria*

Luminescent bacteria, several species of which were described from Sydney by Katz (1891), were rare and confined to sea-water samples. They appeared to lose this property on subculture.

One thus finds a further qualitative differentiation between sea-water and mud forms, and those associated with fish. Once again the preponderance of coloured forms is, as ZoBell says, yellow, followed by orange, then green-fluorescent in fish, and pink to brick-red in sea-water and estuarine muds.

VI. Distribution of Bacterial Species

The classification used in this paper is that set out by Wood (1950*b*). The micrococci follow that of Wood (1952), while the corynebacteria follow that of Kisskalt and Berend (1918); the bacilli and *Pseudomonas* follow Bergey's Manual (6th ed.) as both these genera have recently been critically revised.

The pleomorphic Gram-negative rods, being morphologically identical with a type culture of Gray and Thornton's *Mycoplana*, have been put into that genus. The generic characters used here are morphology, Gram-stain, flagellation, and acid-fastness, while the specific character is pigmentation.

(*a*) Genus *Staphylococcus* Rosenbach

The details of this genus have been considered in a separate paper (Wood 1952), and species-groups have been delimited. The British view that *Staphylococcus* is preferable to *Micrococcus* has been accepted by the author. The strains were, on the whole, fermentative, producing acid from hexoses and disaccharides, but not so frequently from pentoses. They were weakly proteolytic, and the reduction of nitrate was variable. On fish, the pigmented forms represented about 50 per cent. of the cultures, but only about 13 per cent. in sea-water and estuarine muds.

They have not been isolated in investigations on agar digestion or alginate decomposition, but a chitin digester has been isolated by Campbell and Williams (1951).

Staphylococcus candidus Cohn

This species was isolated in 545 out of 813 cultures of staphylococci. Only about 25 per cent. were proteolytic, while 88 per cent. produced acid from glucose and maltose, and 93 per cent. from saccharose. *Staph. candidus* was common in sea-water and estuarine muds at times, and in teleost fish (Table 1) but rare in elasmobranchs, marine muds, and absent on submerged surfaces.

Staphylococcus aurantiacus (Schroeter) Cohn

This species was more proteolytic than the other species, and 77 per cent. of the strains were saccharolytic (90 per cent. fermented lactose and galactose). It appeared in 100 cultures; 89 per cent. of the cultures were from teleost fish, and it was rare in other environments.

Staphylococcus luteus (Schroeter) Cohn

The *luteus-varians* group was relatively inactive (35 per cent. proteolytic and 33 per cent. saccharolytic, i.e., fermented two or more sugars).

This species occurred only in teleost fish (43 cultures).

Staphylococcus varians Migula

Staph. varians was found in 106 cultures, 75 from teleosts, eight from sea-water, and 22 from estuarine muds.

Staphylococcus flavus Trevisan

Only four cultures were isolated from elasmobranchs, so this species is unimportant.

Staphylococcus roseus Flügge

This species occurred in 13 cultures, 10 of them from sea-water, two from marine muds, and one from elasmobranchs. It thus appears to be a part, though a minor part, of the marine flora.

(*b*) Genus *Sarcina* Goodsir

The author does not agree with the inclusion of this genus with *Staphylococcus* as division in two and three planes requires a difference in cell symmetry which is surely fundamental.

The genus is not actively proteolytic, and somewhat less saccharolytic than *Staphylococcus*. It is of minor importance in the sea, giving only 91 cultures out of 2969 (Table 1). There are few motile strains, and most isolates were intensely Gram-positive in young cultures, negative in older ones. Pigmented strains were relatively much more common than in *Staphylococcus*, especially in muds, the chief marine source of the genus. The species isolated were:

Sar. candida, 46 cultures, mainly from sea-water and estuarine muds.

Sar. schaudinii, four cultures from marine muds.

Sar. aurantiaca, 20 cultures mostly from estuarine muds.

Sar. lutea, 14 cultures from sea-water, estuarine muds, and elasmobranchs.

Sar. citrea, seven strains, six from elasmobranchs.

(*c*) Genus *Sporosarcina* Beijerinck

Sporosarcina ureae Beijerinck

The author recorded this motile, spore-forming coccus once off Port Hacking, during the period of the onshore set of the east Australian current (see Wood 1946).

(*d*) Genus *Corynebacterium* Lehmann & Neumann

Corynebacterium is considered by the author to include Gram-positive rods, usually staining irregularly, not acid-fast, with "snapping" cell division. He has taken the step suggested by other authors (Taylor 1942, Taylor and Lochhead 1937) of including *Bacterium globiforme* Conn in this genus, as it shows snapping division in very young cultures (Wood 1950*a*). Kisskalt and Berend (1918) were the first to suggest that non-pathogenic forms of animal origin belong to this genus. In this they were supported by Lehmann and Neumann (1927), and by Jensen (1934). Conn and Dimmick (1947) have created the genus *Arthrobacter* to include the soil bacteria described by Jensen as *Corynebacterium*, and *Bacterium globiforme* Conn. This creation of genera on ecological grounds is undesirable and contrary to the principles of taxonomy. These authors separate the new genus on the basis of a greater variation on morphology, including a tendency to branching, ability to grow without organic nitrogen, weak acid production in sugars, a more variable Gram reaction, and ability to digest gelatin. The marine forms are intergrades between *Arthrobacter* and *Corynebacterium*. They rarely branch, except on synthetic media, show typical palisade formation and "Chinese characters," do not grow readily without organic nitrogen, rarely liquefy gelatin, though about 50 per cent. do slowly form a crater-shaped depression therein. Sugar reactions vary both in the number of sugars attacked and the degree of acidity produced. All cultures tested grew readily in sugar media even if they did not produce acid. This occurrence of intergrades makes Conn and Dimmick's genus unsound.

Coccoid forms were very common—usual in *C. erythrogenes* and in many strains of *C. globiforme*. Cystites, as described by Jensen (1934), and filaments were more common in some strains than in others. Some strains stained with Neisser were morphologically indistinguishable from *mitis* and intermediate strains of *C. diphtheriae*, and many more resembled *C. hoffmanni*. Topping (1937) isolated forms that resemble those of the present author rather than Conn and Dimmick's *Arthrobacter*.

Many strains of *C. globiforme* are motile, and so are a large number of the marine strains identical in all other respects with *Corynebacterium.* Some of Topping's strains were also motile, and motile forms with polar flagella are therefore also included in the present definition of *Corynebacterium.* Clarke and Carr (1951) record a number of motile strains of several soil forms.

Brooks and Hucker (1944) failed to find any correlation of characters which would serve as a basis for classification, stating, "The experimental results have shown the futility of attempting to devise a key system on any but arbitrary grounds, since no degree of correlation could be found between the characters studied." They suggest a classification on morphological, cultural, and physiological grounds, with habitat playing a secondary role. They use groups of characters to separate their species. As far as the author is concerned, from 463 cultures studied in detail, pigmentation is constant, a fact earlier realized by Kisskalt and Berend. Pathogenicity and habitat are less constant, but these and temperature relationships, being used for separating animal parasites, need not be considered here.

The corynebacteria, although not as numerous as the micrococci, appear to play a more important part in the degradation of organic matter in the sea. Strains can attack cellulose and agar, and the majority of strains can decompose urea. All are catalase positive. They grow slowly on gelatin, and only about 30 per cent. liquefy it slowly, mostly forming a crater-shaped concavity in the medium, with a liquefied layer below the colony. It would seem that the difference between this type of liquefaction and that caused by *Bacillus, Pseudomonas,* etc. is that the former is due to a non-diffusible, the latter to a diffusible proteolytic enzyme. On liquid carbohydrate media, the corynebacteria grow well, forming a brittle pellicle, similar to that of *C. diphtheriae,* but may not produce acid. Some, however, do produce acid quite rapidly.

Corynebacterium globiforme (Conn) Wood

Taylor (1938) discusses the variation in soil strains of *Corynebacterium globiforme,* and the author (Wood 1950*a*) has given an illustration of the variation in marine strains. Thirty-two per cent. of strains were motile. This was the most common species of *Corynebacterium* from marine sources (233 cultures out of 463). It formed 72 per cent. of the mud *Corynebacteria,* 80 per cent. of the fouling, 36 per cent. of elasmobranch, and 20 per cent. of teleost flora. It was more common than the pigmented forms except in fish.

Corynebacterium helvolum (Zimmermann) Kisskalt & Berend

This vigorous lemon-yellow species has a very characteristic colony appearance, and its morphology on nutrient agar is very similar to that of *C. diphtheriae.* Twelve per cent. of strains were motile. It was very important in elasmobranch spoilage, as it usually (71 per cent. of the cultures) split urea. Its proteolytic activity was relatively slight (about 14 per cent. liquefied gelatin slowly), carbohydrate breakdown occurred in less than 50 per cent. of the cultures. It occurred in teleost fish, but was rare in sea-water and mud. *Corynebacterium fimi* (*Cellulomonas fimi*) is probably a cellulose-digesting form of *C. helvolum.*

Corynebacterium erythrogenes (L. & N.) Kisskalt & Berend

Its reactions were similar to those of *C. helvolum,* from which it differs only in its bright red fluorescent pigment, and its more constant coccoid habit. Eight per cent. of strains were motile. It was confined to fish, and was not found in sea-water or mud.

Corynebacterium brunneum Kisskalt & Berend

The growth of this species is less luxuriant than that of *C. erythrogenes;* urea was usually split; less than half the strains liquefied gelatin or fermented glucose or other sugars. This species was recorded from elasmobranchs (20 cultures) and rarely from other sources.

Corynebacterium flavum (Orla-Jensen) Wood

This species shows moderate growth on solid media, has the usual pellicle on broth; one strain liquefied agar, but all strains otherwise conformed with the reactions of the genus. Sixteen per cent. of strains were motile. It was distributed sparsely throughout marine environments but was most numerous in teleost fish.

Corynebacterium miltinum Kisskalt

It is usually dark pink to brick-red, with a growth similar to *C. brunneum* or *C. flavum.* The pigment is a different colour from that of *Serratia,* and is far more constant. When motile, the flagella are polar. Gas is never produced from carbohydrates. Reactions are similar in character to those of *C. globiforme.* This species was present in sea-water (12 strains) and estuarine muds (13 strains), and rare in elasmobranch fish.

(*e*) Genus *Mycoplana* Gray & Thornton (Plates 1 and 2)

This genus has already been defined (Wood 1950*a*, 1950*b*). These pleomorphic Gram-negative organisms have been described so often from the sea, and can be found even on glass slides immersed in sea-water, that there seems no doubt that they can be differentiated on morphological grounds alone from the other members of the Pseudomonadaceae. The rods are more robust, stain much more irregularly, as well as being more pleomorphic. The cultures isolated by the author are morphologically identical with a culture of *Mycoplana dimorpha* received from the National Collection of Type Cultures. *Mycoplana* is Gram-negative and has polar flagella, if motile, but resembles the Actinomycetales in general morphology. At times, the filaments of *Mycoplana* seem to flex and straighten, and the cell wall is apparently flexible, though that of the short rod and coccoid forms seems rigid. The cells stain irregularly, the short forms usually being bipolar. There appears to be a life cycle similar to that described by Klieneberger-Nobel (1951) and Dienes and Weinberger (1951) and others for *Streptobacillus moniliformis,* etc. The irregular filaments appear to swell and become clavate or spherical, the deeply staining granules (? mitochondria) become closely aggregated, forming cocci, which later apparently break free from the parent body. The spherical bodies resemble the cystites described by Jensen (1934) for certain Actinomycetales, and seen by the author in some strains of *Corynebacterium.*

The physiological reactions of these organisms are similar to those of *Corynebacterium*—gelatin is liquefied by about half the strains, carbohydrates fermented by more than 50 per cent., utilized by most, if not all, agar is liquefied by a number of strains, and starch is frequently hydrolysed. A few strains attacked cellulose. Chitin (Benton 1935) and alginic acid (Thjøtta and Kåss 1945) are attacked by forms which resemble this genus. The strains tested by the writer were tolerant to poisons such as copper and mercury, and frequently attack phenols. The group appears to be as unstable physiologically as other soil-water bacteria. Pigmentation was used to separate them as it appeared constant.

The strains referred to this genus are included by other workers in *Pseudomonas, Spirillum,* and *Vibrio.* The three latter genera are, in the writer's experience, far less pleomorphic than those encountered in this investigation.

Mycoplana dimorpha Gray & Thornton

The large majority of cultures did not liquefy gelatin. Gray and Thornton (1928) use gelatin liquefaction to demarcate *M. bullata,* but this character is not deemed sufficiently important to be of specific value. Carbohydrate fermentation was feeble, gas was at times produced from nitrates; some cultures attacked cellulose, many hydrolysed starch, and some liquefied agar, especially in media poor in nutrients: amino acids were frequently deaminated. Some of the alginate-decomposing forms isolated by Thjøtta and Kåss (1945) and some of Benton's (1935) chitinovorous strains seem to belong to this species. This was the most abundant species found during the investigation and was represented by 1010 cultures out of a total of 2969. The species was rare in fish (the identification in teleosts is uncertain), but predominated in other environments, including submerged glass slides.

Mycoplana flava Wood 1950

This species formed smooth, shiny, semi-transparent to opaque, bright yellow or orange colonies in agar; growth was moderately abundant; *M. flava* was more reactive than the non-pigmented forms, about 50 per cent. of the strains liquefying gelatin and fermenting carbohydrates. Nitrates were usually reduced to nitrites, nutrient broth was turned brown and viscous, starch was usually hydrolysed, H_2S formed from tryptone broth, and urea was hydrolysed. Ninety-six cultures were isolated, 64 from muds, 19 from sea-water, and seven from submerged glass slides.

Mycoplana rubra Wood 1950

This species formed small, pink colonies on agar, did not liquefy gelatin; some strains fermented carbohydrate, formed H_2S from tryptone broth, and deaminated amino acids. It was commonest in estuarine muds (13 strains), and rare in other environments.

Mycoplana citrea sp. nov.

This is a lemon-yellow species with the characters of *M. dimorpha*. It was isolated from estuarine muds on three occasions.

(*f*) Genus *Bacillus* Cohn

The revision of the genus by Smith, Clark, and Gordon in the 6th edition of Bergey's Manual has been accepted by the author, as it seems adequate to the present purpose. Smith states, "species have been characterized upon a broad basis in the present arrangement on the assumption that one species should not dissociate into another species. Since certain characters are more stable than others, these have been used to establish a *species pattern*. [The italics are Smith's.] Intermediates occur between related species and have been treated as such." This attitude towards the classification of organisms that are mainly saprophytic and variable in their chemical reactions is in line with that adopted by Taylor and the author.

However, *Bacillus* is more stable in its proteolytic activity and carbohydrate fermentation than the genera discussed above.

Bacillus megatherium de Bary

Shadow forms were frequent, and most cells were vacuolate and irregular in shape. This species was not common, but was found in teleosts and estuarine muds.

Bacillus sphaericus Neide

This species preferred a microaerophilic environment. Half the strains decomposed urea, some attacked carbohydrates, reduced nitrate, and formed H_2S. It was fairly common in estuarine muds and rare in other environments.

Bacillus subtilis Cohn

B. mesentericus is included here. *B. subtilis* was the commonest member of this genus in marine cultures (176 strains). It was rare in elasmobranchs and on submerged plates, but quite frequent in teleosts, sea-water, and estuarine muds.

Bacillus cereus Frankland & Frankland

This species occurred in teleost fish, but arborescent colonies were rare.

Bacillus lentus Gibson

The strains isolated by the writer and assigned to this species were on the whole somewhat more reactive than those isolated by Gibson. Nitrates were slowly reduced by two strains, and H_2S was formed from tryptone broth; peptone and amino acids were deaminated. This species occurred in muds and on submerged plates.

In addition, three strains of an orange-yellow, and 11 of a brick-red to pink spore-former of the *subtilis* type were isolated from sea-water and estuarine muds. Two bright red strains with terminal spores, not liquefying gelatin but decomposing urea, were also isolated from mud. They resembled *B. sphaericus* Neide.

Pigment production has hitherto rarely been recorded in the genus *Bacillus*, so its value as a specific character cannot be assessed. In the cultures isolated, pigmentation was constant and distinct, and, by analogy with other genera, the creation of three species for these cultures would be justified. However, it is more difficult to recombine species than to create them, so the strains are merely recorded at the moment.

Also recorded by the author from teleost fish (Wood 1940) are *B. subtilis* var. *niger*, *B. pumilis* (*B. parvus*), together with the uncertain forms *B. lautus*, *B. amarus*, and *B. nitus*.

(*g*) Genus *Pseudomonas* Migula

This genus as differentiated from *Mycoplana* was isolated frequently from teleosts, more rarely from elasmobranchs, and rarely from sea-water and muds. The fluorescent strains occurred only twice from sea-water, and were not found in muds. They are exceedingly common in river water, and are suspected of causing diseases in trout in Tasmania. The cultures isolated all produced acid in glucose and in no other sugar, were frequently proteolytic, and all except *P. fragi* attacked urea.

The following species were recorded:

Pseudomonas fluorescens Migula, confined to fish.

Ps. putida (Trevisan) Migula, occurred in fish, two cultures from sea-water.

Ps. chlororaphis Guignard & Sauvageau, rare in fish.

Ps. desmolyticum Gray & Thornton, occurred in elasmobranchs.

Ps. boreopolis Gray & Thornton, rare in elasmobranchs.

Ps. fragi (Eichholz) Huss, one strain from elasmobranchs.

Ps. viscosa (Frankland & Frankland) Migula, was common in spoiling teleost fish; rare in sea-water.

Ps. pavonacea Levine & Soppeland. Only found in teleost fish.

Ps. mildenbergii Bergey *et al.* Fish muscle and market only.

Ps. convexa Chester, occurred once in mullet slime.

Of these species, those found in the gut or slime of fish must be regarded as marine or estuarine, but those occurring only in flesh may provisionally be omitted from the marine flora. These include *Ps. mildenbergii* and *Ps. chlororaphis.*

(*h*) *Other Genera*

Genus *Proactinomyces* Jensen

Two unidentified strains were isolated from estuarine muds.

Genus *Actinomyces* Harz

Three strains were isolated from teleost fish, one from estuarine muds, and two from sea-water. The species were not identified.

Genus *Proteus* Hauser

Eight strains of *Proteus vulgaris* were isolated from shark flesh (trawler caught). They may not have been of marine origin.

Genus *Enterobacter* Rahn

Peritrichous Gram-negative forms were rare in marine environments, and are probably adventitious. Three strains of *E.* (*Serratia*) *marcescens* and seven strains of the *coli-aerogenes* group were isolated from mullet and from sea-water close to shore.

(*i*) *Yeasts*

Twenty-seven strains of an unreactive pink yeast, three white, and two black yeasts were isolated from fish, sea-water, and mud.

Bacterial Flora from Marine Sources (*Fig.* 7)

It will be seen from Table 1 that the flora of each of the six environments studied, namely teleost fish, elasmobranch fish, sea-water, estuarine muds, marine muds, and submerged surfaces, has a quantitative and qualitative difference in the genera represented. The bacterial flora of fish differs considerably from that of sea-water and muds, which have much in common (Fig. 7). In each the predominant forms are the Gram-negative pleomorphic forms recorded as *Mycoplana* and relegated by other writers to *Pseudomonas*, *Vibrio*, and *Spirillum. Pseudomonas* is rare, except in fish, and is abundant in these only in the later stages of spoilage. The genus *Bacillus* is present in all biocoenoses. Two morphological types are usual, rounded rods with even central spores (*B. subtilis* type) and long, thin rods with swollen terminal or subterminal spores (*B. sphaericus*). No clostridia were found in any environment in this investigation. *Corynebacterium* is present in approximately the same percentage in teleost fish, sea-water, and estuarine mud.

Taylor (1942) records from lake water 95.5 per cent. of Gram-negative rods, 3.8 per cent. of Gram-positive rods, and 0.7 per cent. of cocci. From soil, Taylor and Lochhead (1937) record 42.7 per cent. of *Corynebacterium-Mycobacterium*, 36.1 per cent. of Gram-negative forms,

TABLE 1

DISTRIBUTION OF SPECIES OF AEROBIC HETEROTROPHS ISOLATED FROM SIX MARINE SOURCES

The total number of isolations from each source is arbitrary, but the relative number of each species and genus can be compared for different environments

	Teleosts	Elasmobranchs	Sea-water	Estuarine Muds	Marine Muds	Submerged Surfaces	Totals
Staphylococcus Rosenbach							
Staph. candidus	197	15	100	232	1	0	525
Staph. aurantiacus	89	5	1	5	0	0	100
Staph. luteus	43	0	0	0	0	0	43
Staph. varians	75	1	8	22	0	0	106
Intermediate group							
Staph. flavus	0	4	0	0	0	0	4
Staph. roseus	0	1	10	0	2	0	13
Total *Staphyloccocus*	404	28	119	259	3	0	813
Sarcina Goodsir							
Sar. candida	1	4	10	31	0	0	46
Sar. schaudinii	0	0	0	0	4	0	4
Sar. aurantiaca	1	4	1	14	0	0	20
Sar. lutea	1	4	3	6	0	0	14
Sar. citrea	0	6	0	1	0	0	7
Total *Sarcina*	3	18	14	52	4	0	91
Sporocarcina Beijerinck							
S. urea	0	0	1	0	0	0	1
Corynebacterium (Lehmann & Neumann)							
C. helvolum	18	51	3	4	0	0	76
C. globiforme	26	59	38	72	3	38	236
C. erythrogenes	17	24	0	0	0	0	41
C. brunneum	0	20	3	4	0	0	27
C. flavum	22	6	8	8	0	8	52
C. miltinum	0	2	12	13	4	0	31
Total *Corynebacterium*	83	162	64	101	7	46	463
Mycoplana Gray & Thornton							
M. dimorpha	?	7	417	467	40	79	1010
M. flava	?	6	19	64	0	7	96
M. rubra	?	1	2	13	2	1	19
M. citrea	?	0	0	3	0	0	3
Total *Mycoplana*	?	14	438	547	42	87	1128
Bacillus Cohn							
B. megatherium	11	0	0	8	0	0	19
B. sphaericus	0	2	6	36	0	1	45
B. subtilis	49	2	41	83	0	1	176
B. lentus	0	2	1	11	0	5	19
Yellow and red forms	0	0	4	10	0	0	14
Total *Bacillus*	60	6	52	148	0	7	273
Pseudomonas Migula							
Ps. fluorescens	16	9	0	0	0	0	25
Ps. putida	18	4	2	0	0	0	24
Ps. chlororaphis	1	1	0	0	0	0	2
Ps. desmolyticum	0	11	0	0	0	0	11
Ps. boreopolis	0	3	0	0	0	0	3
Ps. fragi	0	1	0	0	0	0	1

TABLE 1 (*Continued*)

	Teleosts	Elasmo-branchs	Sea-water	Estuarine Muds	Marine Muds	Submerged Surfaces	Totals
Ps. viscosa	59	0	3	0	0	0	62
Ps. pavonacea	6	0	0	0	0	0	6
Ps. mildenbergii	3	0	0	0	0	0	3
Ps. convexa	1	0	1	1	0	0	3
Other spp.	2	0	0	0	0	0	2
Total *Pseudomonas*	106	29	6	1	0	0	142
Proactinomyces Jensen	0	0	0	2	0	0	2
Actinomyces Harz	3	0	2	1	0	0	6
Proteus Hauser	0	8	0	0	0	0	8
Enterobacter marcescens	2	0	1	0	0	0	3
E. coli-aèrogenes	5	0	2	0	0	0	7
Yeasts	13	1	7	11	0	0	32
Grand totals	679	266	706	1122	56	140	2969

3-8 per cent. of cocci, and 3-8 per cent. of spore-formers, while Topping records 73.1 per cent. of Gram-positive rods and 26.7 per cent. of Gram-negative rods (Fig. 7).

Figure 7 calls attention to certain relationships between the floras of certain marine and terrestrial environments. Although lakes have a predominantly Gram-negative rod flora, the proportion of Gram-positive rods and cocci is the same as in marine muds, sea-water, estuarine muds, and the slime and gills of teleost fish. The existence of this common character suggests that these floras have a common origin. There is also a similarity, which is brought out in the diagram, between floras of soil, estuarine mud, and trawler-caught fish, which last, strangely enough, is close to and possibly identical with that of estuarine mud: it is obviously a marine-type flora, modified somewhat by its peculiar environment. The flora of elasmobranch fish lies in the soil region, bearing little relationship to the marine-type flora. The affinity with soil bacteria suggested in this diagram is confirmed by the predominance of *Corynebacterium* in this milieu.

VII. MARINE ENVIRONMENTS

(*a*) *Sea-water*

The majority of cultures from sea-water consisted of Gram-negative pleomorphic bacteria of the genus *Mycoplana,* most of which were non-pigmented; these were followed by the cocci, and once again the majority were not pigmented. There were occasions, however, when pigmented forms predominated, but it could not be shown that these occurrences were seasonal. The majority of bacteria in sea-water were found to be adsorbed on particles (see above) and tests on adsorbed and unadsorbed bacteria showed that there was a marked increase of activity after adsorption, i.e. on diatomaceous earth or sterile mud. The question of whether there are sufficient bacteria in the sea to bring about the changes necessary for the release of inorganic nutrients is still an open one, though the evidence suggests other agencies—catalysts of presumably bacterial origin—are available to assist the bacteria. This question was raised by Kreps (1934) and by Keys, Christensen, and Krogh (1935), who suggested that there are free enzymes in the sea. Their idea was based on the activity of water sterilized by Seitz filtration or by mercuric chloride. The latter is an enzyme poison, so seems to rule out the usual type of organic enzyme.* The author has found evidence of activity in muds autoclaved at 15 lb. pressure for 20 min., which also rules out ordinary enzymes. Two theories to explain this phenomenon seem possible (Wood 1950*c*):

(1) Non-specific organic or inorganic catalysts may be produced by bacteria and adsorbed by particles in the sea. These substances would then be cumulative, and not directly related to the bacterial population.

(2) Bacteria may produce conditions favouring certain reactions and these reactions may be catalysed by substances in the substrate. Particles in the ocean would then serve not only to facilitate bacterial reproduction but would increase the surface available for the action of catalysts. The reaction would continue in terms of mass action as long as one of the products was removed by adsorption or precipitation, and as long as conditions were unaltered.

In either way, small numbers of bacteria could produce chemical changes out of all proportion to the population. In the presence of plankton swarms, conditions are suitable for the great bacterial activity that occurs, and would also facilitate the activity of enzymic or catalytic processes.

(*b*) *Marine Muds*

The continental shelf: material for this study was collected by F.R.V. *Jay Bee* from the Division's hydrological station 5 and 10 miles east of Jibbon Cape, Port Hacking. There is little mud in this area, the bottom consisting mainly of sand. The station is situated at the southern end of the Botany trawling ground, now practically abandoned by trawlers owing to poor catches. The sandy bottom was found to be sterile as regards heterotrophs growing on sea-water agar, but the muds produced a flora consisting chiefly of *Mycoplana* together with *Corynebacterium globiforme* and *Staphylococcus candidus* (all non-pigmented), together with red staphylococci and corynebacteria. Gram-negative organisms totalled 76.4 per cent. There were no yellow or brown forms. As red forms are rare, and yellow are common in fish spoilage, it seems very doubtful whether the fish flora is derived from the feeding grounds (Fig. 7). This result was unexpected. No strict anaerobes were isolated from this environment, and the species found were also obtained from the sea.

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* Since this paper was written, Oliver (1952) has shown that at least some bacterial enzymes (e.g. decarboxylases) are resistant to 100°C. for 1 min., to 0.2 per cent. $HgCl_2$, to 1 per cent. "Centrimide", and lose little, if any, activity over 7 days.

(*c*) *Estuarine Muds*

The estuarine muds examined were those of the oyster-fattening area of Botany Bay. The samples were of intertidal muds at surface and at 2 ft. All the heterotrophs were facultative anaerobes, but no true anaerobes were found except for the sulphate-reducing bacteria. This result is at first sight rather surprising in the light of the reducing nature of the substrate. However, it has recently been found by Mr. D. J. Rochford of this Division that there is a minimal oxygen layer not far below the surface of these muds, and that the oxygen tension increases above and below this layer, with consequent oxidation of the sulphide in the surface zone. That there are no obligate or strict anaerobes at the surface is not surprising on consideration of the photosynthetic activity there. It can be shown by placing a sealed jar of reduced mud in the light that the sulphide is rapidly oxidized as a result of the photosynthetic activity of organisms dormant in the mud, since the black sulphide of iron completely disappears in the illuminated area provided that the silt fraction is low. It appears also from this type of experiment that agar and cellulose digesters acting on the organic matter on the top layer of mud can produce reducing conditions below it which allow the action of the sulphate reducers. The fact that sulphate reduction will occur if glass beads (ballottini) or diatomaceous earth are substituted for sand or mud shows that the sulphur and iron are derived from the interstitial water, though they will, in fact, be concentrated in the mud by adsorption.

The flora of estuarine muds consisted of *Mycoplana* and the cocci, chiefly staphylococci with a few motile sarcinae; *Corynebacterium* and *Bacillus* were relatively common, and in the latter genus were yellow and red forms, which at times were very conspicuous on the poured plates. Non-pigmented forms predominated in this environment.

(*d*) *Submerged Surfaces*

The bacterial fouling of submerged surfaces is not as great in Australian waters as it was shown to be in California by ZoBell and his co-workers (ZoBell 1939) who found 11,570,000 bacteria per sq. cm. in 72 hr., whereas the author (Wood 1950*d*) found a maximum of 281,500 per sq. cm. at The Spit (Sydney Harbour) in the same period. Later tests carried out recently near the explosives buoy in Sydney Harbour near the main channel confirmed previous findings that the attachment of algae and animal larvae is independent of bacterial film. Clumping of bacteria round, but not touching, algal spores and detrital material was usual, so it would appear that the attachment of these bacteria followed that of the other material. It was also found that bacterial film, alive or dead, did not increase the weight of subsequent growth, but that live primary algal or diatom film did accelerate such growth. It was found, however, that a primary film of bacteria did tend to form on slides painted with mercury paints, and submerged for a month. This film was zoogloeal, and quite thick. Bacteria isolated from submerged slides were capable of withstanding up to 250 p.p.m. of copper as copper sulphate and 100 p.p.m. of mercury as mercuric chloride (Appendix VI).

The fouling flora consisted chiefly of *Mycoplana,* followed by *Corynebacterium,* with an occasional *Bacillus.* The pleomorphic *Mycoplana* strains were easily recognized on the plates, but coccoid forms were apparently *Corynebacterium.* Stalked bacteria as described by ZoBell (1946) and Henrici (1935), and some forming arborescent pattern on the plates were occasionally met with, but failed to grow on the media used.

(*e*) *Fish*

As stated in previous papers (Wood 1940, 1950) there are many differences between the floras associated with teleost and elasmobranch fishes. There is, for example, no evidence of a succession of genera in the spoilage of elasmobranchs as there is in the teleosts. That this is characteristic of teleosts was shown by placing live fish in sterile test tubes (Wood 1940) and allowing them to spoil. The succession followed exactly the same pattern as it did in ordinary spoilage. This also showed that the spoilage flora was essentially derived from the surface, gut, and gills of the fish itself, i.e. that it was derived from a marine environment. This is confirmed in Figure 7. The succession is probably an example of metabiosis in which each organism prepares the milieu for the succeeding one.

There is also a marked difference in the ratio of different genera and species associated with teleosts and elasmobranchs, as is shown in Figure 7.

The cultures listed under *Mycoplana, Achromobacter,* and *Flavobacterium* were Gram-negative rods, but the identity of the last two is uncertain. The Gram-positive rods found in teleost fish are now assigned to *Corynebacterium,* to which genus they undoubtedly belong. A number of the so-called *Achromobacter* and *Flavobacterium* strains were pleomorphic and belong to the group now assigned by the author to *Mycoplana,* but as the cultures were lost no direct comparisons can be made. That pleomorphism is highly characteristic of marine bacteria was only slowly realized after attempts to "purify" a number of such cultures had failed.

The floras of teleosts and elasmobranchs are undoubtedly related to the constitution of the substratum. In teleosts, fish protein was lysed by 38 per cent. of staphylococci, 18 per cent. of *Achromobacter,* 39 per cent. of *Flavobacterium* and *Pseudomonas,* 5 per cent. of *Corynebacterium globiforme,* and 51 per cent. of *C. helvolum.* Few organisms, mainly *Pseudomonas,* produced ammonia from fish protein. With elasmobranchs, 89 per cent. of the strains isolated produced ammonia from shark agar and from urea media; 40 per cent. could use urea as the sole source of carbon and more than 70 per cent. could use urea as a source of nitrogen; 99 per cent. possessed a urease, and 79 per cent. hydrolysed protein and produced ammonia from peptone and meat extract. Thus most of the organisms isolated from elasmobranchs appear to possess a urease and many of them also protease. There was variation in the reactions of different strains of the same species and no genus could be singled out for its reactivity in this respect, all the genera isolated showing a considerable range of activity. It was not possible to differentiate between the reactions of strains isolated from the skin or from the muscle of elasmobranchs, so it must be concluded that these environments act as an enrichment medium to select the flora found in them.

Carbohydrate fermentation is exceedingly variable in all the marine strains. In the genera *Corynebacterium* and *Mycoplana*, about 50 per cent. of each species were actively fermentative, maltose and saccharose being fermented more frequently than glucose. The cocci were much more frequently fermentative, the percentage of strains fermenting glucose, maltose, and saccharose being of the order of 70-90 per cent.

It may be concluded that bacteria living on the surfaces (slime, shagreen, etc.) of fish are a specialized section of the marine flora occasioned by the environment. The flora on teleosts is less proteolytic and, generally, less reactive than that on elasmobranchs which accounts, at least in part, for the more rapid spoilage of the latter. We have therefore specialized marine floras in specific situations. The same applies to the flora of the Phaeophyceae, which is enriched with alginate digesters and mannitol fermenters, and that of the Rhodophyceae, which gives an unusually high count of agar digesters. Chitinoclastic bacteria are largely restricted to plankton swarms, crustaceans, and bottom muds in which the chitin-producing organisms are decomposed.

No attempt has been made to classify the autotrophic bacteria as the relationships of these organisms to their heterotrophic counterparts have not yet been worked out.

VIII. Bacteria as Food

Bacteria serve as food for ciliates and holozoic flagellates in marine muds, as can be determined by microscopic study. They abound in the reduced zones of muds with redox potential (Eh) as low as —150 mV. as well as in the oxidized zone. It seems probable that, by ingesting autotrophic bacteria in the reduced zone, they can be an important factor in the translocation of nutriments in muds. The subsequent ingestion of these organisms by mullet, oysters, and other shellfish would complete the nutritional chain.

Bacteria are also used as food directly by invertebrates and vertebrates.

ZoBell and Feltham (1938) showed that *Mytilus* can ingest and digest bacteria, so also can certain crabs and gephyrean worms. Professor T. Imai of Tohoku University, Sendai, Japan, maintains that bacteria are necessary to feed the larvae of *Ostrea gigas,* and uses them in his cultures.

He maintains that, in nature, these larvae derive their food from bacteria and monads associated with decomposing *Zostera*. The author has found that the Australian oyster thrived better if the diet included bacteria, and that those fed on bacteria spawned when the others did not. However, if the bacteria become too numerous, the oysters sicken and die, owing to the reduction of the oxygen tension by the bacteria. Professor Baas Becking has suggested that the brood of *Chanos chanos* (milkfish) may also feed on bacteria. As the direct count of bacteria in estuarine silt fractions is of the order of 1×10^9 per cc., these organisms may be an important direct food of mullet, which ingests large quantities of this silt material. A mullet with 2 cc. of mud in its gut would have ingested about 4 cu. mm. of bacteria.

IX. Conclusions

It will be seen from this paper, as from ZoBell's monograph, that the knowledge of even the heterotrophic bacteria contains large gaps, and is often the subject of speculation rather than of factual knowledge. One of the reasons for this slow progress is that each worker has to work out his own methods for each step so that a short advance means a great deal of thought and experimentation. The writer has recently used with success the metabiotic approach suggested by Professor Baas Becking, wherein mixed cultures of bacteria are used to reproduce phenomena which occur naturally, so that conditions can be controlled and studied. This method also requires means of biological assay of products which cannot be assessed directly by chemical means.

One may also conclude that bacterial action in marine environments is, in its quantitative aspects, dependent on adsorption phenomena, and that future studies may well be directed to conditions for adsorption and desorption of bacterial enzymes and catalysts, and of metabolites in the sea.

Something is known about the kinds of bacteria in the sea, their probable numbers, and their metabolism. There is also considerable information concerning their reactions *in vitro*. We cannot, however, answer such questions as whether nitrogen fixation by bacteria is important, or what is the actual balance between nitrification and denitrification. The methods suggested above seem promising for this much-needed work.

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APPENDIX I

Results of Adsorption Experiments

Suspensions of marine bacteria 18 hr. old were diluted, centrifuged at 2,000 r.p.m. to remove clumps, and counted in a haemacytometer, the counts of the suspensions being (*a*) 37,500; (*b*) 665,000; (*c*) 5,750,000 per ml.

These suspensions were then shaken for ½ hr. with the silt fractions of estuarine muds of which approximately 30 per cent. of the particles were less than 10 μ in diameter. The finer particles of the mud were counted in the haemacytometer cell, the number of such particles being:

	A	*B*	*C*
2-10 μ	32,500	140,000	6,000
1-2 μ	120,000	120,000	115,000

The suspensions were again centrifuged at 2,000 r.p.m. for 15 min. and the unadsorbed bacteria in the supernatant were counted.

In dilution (*a*) 95.9 per cent. of bacteria were adsorbed in each mud; in dilution (*b*) 99.8 per cent. were adsorbed in muds *A* and *B* and 98.9 in *C*; while in dilution (*c*) 91.2 and 92 per cent. were adsorbed in muds *A* and *C* and in *B* only 65.0 per cent. In this case, however, clumping of the bacteria in the supernatant was observed.

It would appear that, as Rubentschik observed, there is an optimum concentration for the adsorption of bacteria, in this case below 1×10^6.

The experiments showed that, as other writers have observed, adsorption is of outstanding importance in studying marine phenomena.

These results were confirmed by examining stained samples of actual mud where in all cases over 90 per cent. of the bacteria observed were adsorbed on particles. The numbers of bacteria adsorbed on each particle did not depend on the size of the particle though it was frequently observed that more bacteria were adsorbed on particles showing some organized structure.

Particle counts of sea-water taken 5 miles off Jibbon Cape showed:

2.5-5 μ, 1800 per ml.; 5-10 μ, 800 per ml.; and over 10 μ, 200 per ml.

Single bacteria were seen adsorbed on some of these particles and no free bacteria were observed.

APPENDIX II

Relation between Plate and Direct Counts in Dilutions of Bacteria

Platings on nutrient agar were made of several dilutions of a bacterial suspension by the usual dilution method using autoclaved sea-water as diluent and the results compared with haemacytometer counts of the original dilutions.

The results were:

Plate Count	Direct Count
3,000	15,000
75,000	445,000
400,000	1,700,000
1,200,000	10,000,000
5,000,000	100,000,000

This suggests that the relationship between direct and plate counts improves with the decrease of the number of bacteria present. A repetition of the experiment showed that, when direct counts were below 1×10^6, the plate count showed $\frac{1}{4}$-$\frac{1}{8}$ of the total count, when but direct counts showed over 1×10^7 the discrepancy rose sharply. Direct counts of muds compared with plate counts in sea-water nutrient agar showed that plate counts gave 1/100-1/1000 of the direct counts. These counts were of surface muds where the direct counts were of the order of 1×10^8 to 1×10^{10}. No constant relationship could be demonstrated between direct and plate counts at this population level.

APPENDIX III

Aerobic and Anaerobic Bacteria in the Sea

A study of the literature shows a number of references to "anaerobic" heterotrophic bacteria in marine muds. However, there is no evidence that these bacteria are strict anaerobes. The author, as a routine, set up parallel plate cultures from muds in hydrogen in McIntosh & Fildes jars and in air. The counts in these plates were equal within the limits of error of plating techniques and all colonies selected at random from aerobic and anaerobic plates grew equally well in either milieu. It does not appear therefore that strict anaerobes are important among the heterotrophic bacteria in the mud; the author has not found evidence of the existence of such strict anaerobes.

APPENDIX IV

The Bactericidal Property of Sea-water

A freshly isolated culture of sea-water bacteria and one of soil forms were used in these tests. Each was from on sea-water and freshwater nutrient agar for 48 hr., diluted in autoclaved sea-water. Then each culture in appropriate dilutions was shaken for 30 min. with fresh sea-water. Shaking was continued for another 90 min. and the cultures were again plated.

The sea-water organism cultured on freshwater agar was reduced in number from over 1000 to 4 per ml. in $\frac{1}{2}$ hr. and to 2 per ml. in 2 hr. Grown in sea-water agar the number was reduced from over 1000 to 28 per ml. in $\frac{1}{2}$ hr. and to 2.5 per ml. in 2 hr.

The soil organism cultured on sea-water agar was reduced from over 1000 to 20 per ml. in ½ hr. and to 13 per ml. in 2 hr.; grown in freshwater agar it was reduced from 640 per ml. to 26 per ml. in ½ hr. and to 8 per ml. in 2 hr.

The same cultures plated directly from dilutions (*a*) in contact for 2 hr. with autoclaved sea-water, (*b*) sea-water filtered through Jena sintered glass filters of porosity 4 (*c*) (bacteria proof) and 3 (to remove protozoa) gave these results:

(*a*) Control—12 per plate.
(*b*) Autoclaved sea-water 16.3 per plate.
(*c*) Bacteria-proof Jena filter 16.3 and 16.5 per plate (2 tests).
(*d*) Porosity 3 Jena filter 19.8 and 27.0 per plate (2 tests).

I.e. there was an increase in growth, possibly due to multiplication in the filtered sea-water, and to bacteria which had passed through the No. 3 filter.

APPENDIX V

Variation in Reactions of Marine Bacteria

Two cultures of *Staphylococcus* and two of *Corynebacterium* were purified by single cell technique—streaking dilutions on agar-coated 3 by 1 in. microscope slides, selecting isolated cells microscopically by using the stage vernier, and, after incubation, subculturing from the colonies originating from these cells. From the pure cultures, 10 colonies of each were selected and sown to differential media (S.A.B. Manual of Methods). The results were as follows:

	Nitrate	Glucose	Lactose	Sucrose	Maltose	Mannite	Laevulose	Glycerol	Galactose	Inulin	Salicin	Xylose	Raffinose	Milk
Orig.	+	A	A	A	A	A	A	—	—	—	A	—	—	Pept. alk.
Staphylococcus A	5	10	2	10	10	10	10	10	7	0	10	4	0	5 Alk. 5 Ac. Decol.
	+	A	A	A	A	—	A	A	A	—	—	—	—	Acid, coag. 10
Staphylococcus B	9	10	2	10	10	10	10	10	9	1	10	8	3	Acid, no coag.
	+	—	—	—	—	A	—	—	—	—	—	—	—	Alk.
Corynebacterium C	10	4	0	2	2	2	2	1	1	0	5	1	2	Alk. 8
	+	—	—	—	—	—	A	A	—	—	—	—	—	Alk.
Corynebacterium D	10	4	1	1	2	1	3	0	3	0	7	0	0	Alk. 9

In the *Staphylococcus* cultures, nitrate reduction was variable, while the reactions in the sugars, glucose, lactose, sucrose, maltose, laevulose, and salicin were constant. Reactions on the other sugars varied to a greater or lesser extent. Milk reaction varied. If we assumed *A* and *B* to be the same species we could delineate it by its reactions on five sugars, but a study of a large number of *Staphylococcus* cultures showed a random variation in the sugars fermented, so that the use of sugar reactions in taxonomy does not seem justified.

The corynebacteria showed constancy in nitrate reduction and variation in all other tests. Other tests, however, showed variations in nitrate reduction in subcultures of the same strain.

APPENDIX VI

Tolerance of Bacteria to Copper and Mercury

In order to determine the tolerance of marine bacteria to copper and mercury, the common poisons used in antifouling paints, copper paints of high and low leaching rates, and a mercury paint were exposed in the sea for 14 days with an unpainted glass plate as control.

Each plate was swabbed in the laboratory with sterile cotton wool and streaked on nutrient agar slopes containing mercury (1, 10, and 100 p.p.m.) or copper (2.5, 25, and 250 p.p.m.) with non-toxic agar as control.

Growth occurred on mercuric chloride agar (100 p.p.m. Hg) of the cultures isolated from all but the high leaching rate copper plate, and on copper sulphate agar to 25 p.p.m. Cu of cultures from the low leaching rate mercury and copper plates. The high leaching rate copper paint gave growth only on the slope with 1 p.p.m. of mercury.

Pure cultures were then made from these slopes and included Gram-positive sporing rods (pink), Gram-negative pleomorphic rods, and cocci. Of 22 cultures isolated 12 grew on 1 p.p.m., 7 on 10 p.p.m., and 7 on 100 p.p.m. mercury, and 15 on 2.5 p.p.m., 10 on 25 p.p.m., and 4 on 250 p.p.m. copper. The seven cultures most tolerant of mercury were also tolerant of copper.

On one plate painted with the mercury paint, a zoogloeal film developed after 1 month's immersion in the sea, accompanied by a breaking down of the paint surface. This was the only linseed-oil-base paint in the tests, the copper paints being resin-base paints.

THREE NEW STOMATOPODA (CRUSTACEA) FROM EASTERN AUSTRALIA

By W. Stephenson*

(*Manuscript received October* 23, 1952)

Summary

The following new species are described and figured: *Squilla granti* from Moreton Bay, Queensland; *S. terrareginensis* from north Queensland; and *S. mcneilli* from deep water off the New South Wales coast. Justifications are given for the elevation of *S. scorpio* var. *immaculata* Kemp 1913 to specific rank.

Introduction

In a previous publication (Stephenson 1952) an undescribed stomatopod in the collections of the Zoology Department, University of Queensland, was mentioned. Since then, specimens of two other undescribed species have been examined in the collections of the Australian Museum, Sydney. These three species are now described. The second (*Squilla terrareginensis*) resembles *S. scorpio* Latreille 1825 to a very marked degree, but is readily distinguishable by inconspicuous characters. It would appear that, in this section of the genus, species show close affinities and that *S. scorpio* var. *immaculata* Kemp 1913 should be elevated to the rank of a full species.

Since the publication of Kemp's (1913) monograph on the group there have been several alterations in synonymy and numerous additions to the lists of Australian species. These changes will be considered in a later publication.

CORRIGENDUM

Page 201, third line of third paragraph of the Introduction; for "including", read "excluding".

1948 *Squilla microphthalma* Hynd, B.Sc. Hons. Thesis, Univ. Qd. (unpublished) pp. 84-5.

Material

All specimens were trawled or dredged from shallow water in Moreton Bay, Queensland, and unless otherwise stated are held in the Museum of the Department of Zoology, University of Queensland.

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* Department of Zoology, University of Queensland.

Holotype.—♂, 61 mm., 5½ miles NNE. Woody Point Pier, 3.i.1951, E. Grant (muddy sand, 12 m. depth) (Queensland Museum).

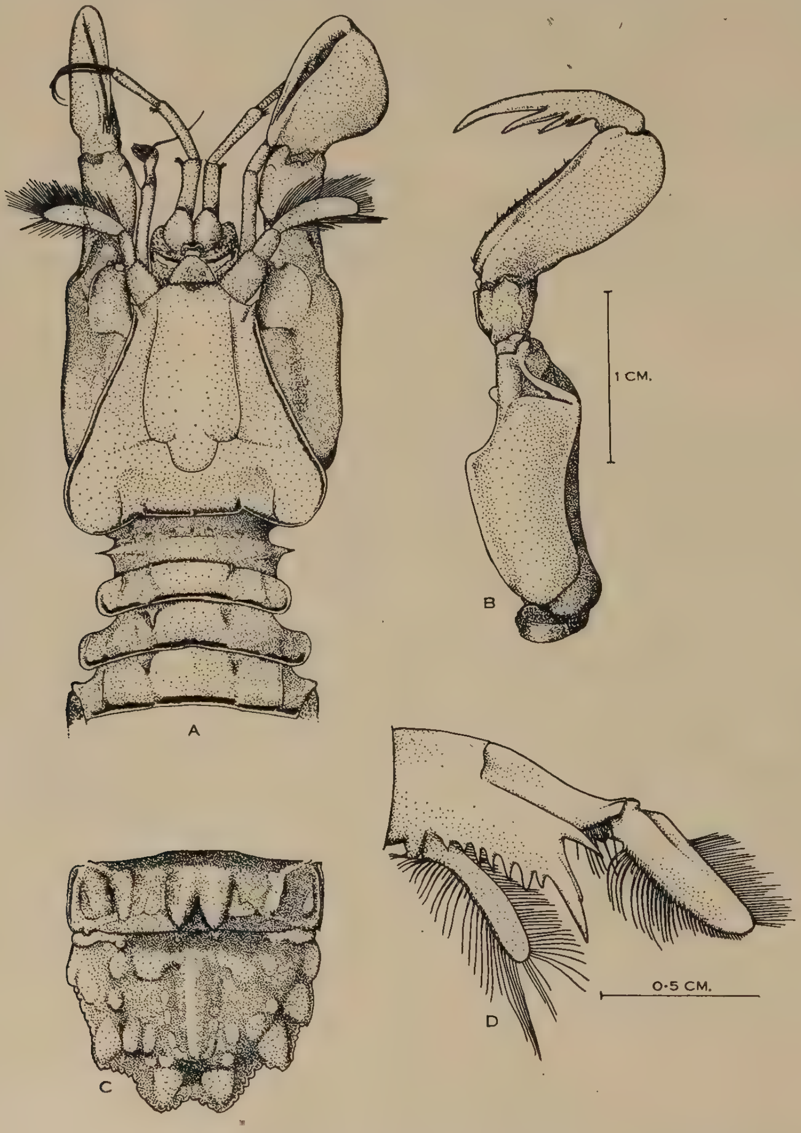

Fig. 1.—*Squilla granti*, sp. nov., holotype.
A, Dorsal view of anterior half of body.
B, External view of right raptorial claw.
C, Dorsal view of sixth abdominal somite and telson.
D, Ventral view of left uropod, at a different magnification.

Allotype.—♀, 46 mm., 3 miles S. Woody Point Pier, 20.xii.1951, E.G. (sandy mud, 5-6 m. depth) (Queensland Museum).

Paratypes.—Males, 62 mm., 4½ miles E. Scarborough Pier, 5.viii.1950, E.G. (heavy mud, 12 m. depth) (Queensland Museum) ; 60 mm., 65 mm., details coll. as holotype (Australian Museum) ; 61 mm., details coll. as holotype (both raptorial claws missing) ; 57 mm., 3 miles S. Woody Point Pier, 10.xi.1951, E.G. (sandy mud, 6 m. depth) (right raptorial claw missing) ; 65 mm., Redcliffe area, Dec. 1951, A. Keone; 64 mm., 3 miles NE. Woody Point Pier, 9.viii.1952, E.G. (sandy mud, 9 m. depth).

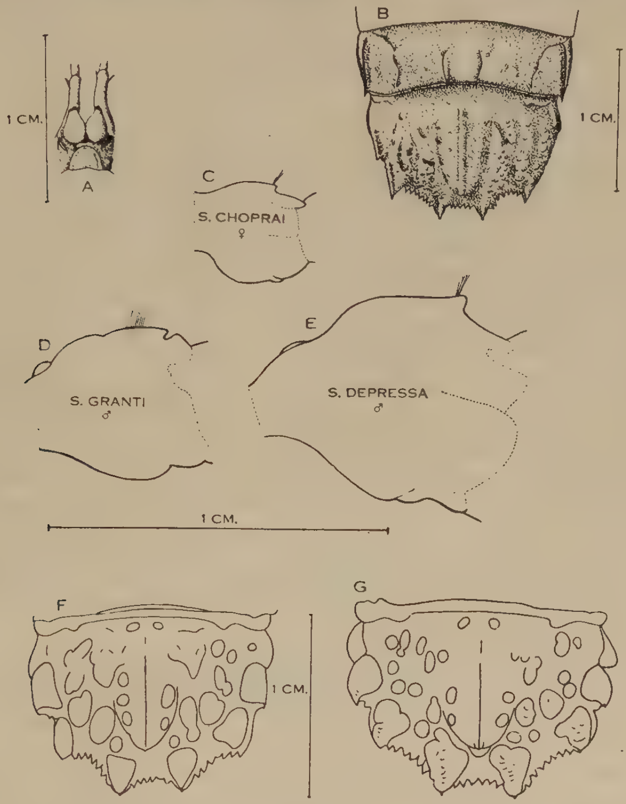

Fig. 2.—*A*, Dorsal view of rostrum, eyes, etc. of allotype of *Squilla granti.*
B, Dorsal view of sixth abdominal somite and telson of allotype of *S. granti.*
C, External view of right raptorial carpus of a female paratype of *S. choprai.*
D, As *C*, but male paratype of *S. granti.*
E, As *C*, but male specimen of *S. depressa* (from Moreton Bay).
F, *G*, Ornamentation of telson of two paratypes of *S. granti.*

Female, 39 mm., Scarborough, 26.v.1913 (bearing Hynd's identification *"Squilla microphthalma* M.—Edw.") (Australian Museum).

Diagnosis

Cornea very small, its breadth only about ½ the total length of the eye, which is itself small and barely reaching ½ way along the basal segment of the antennular peduncle. The anterolateral angles of the carapace are spinous. There is no mandibular palp, and no black spot on the distal ½ of the proximal segment of the expodite of the uropod.

Named after Mr. E. Grant, who has collected the vast majority of existing material.

Description

Eyes.—Eyestalks short and broad, length just less than ½ that of the basal segment of the antennular peduncle, maximum breadth about 60 per cent. of the combined length of stalk and eye. Cornea black, indistinctly bilobed, with the maximum breadth in a dorsolateral direction. In males, this breadth is about 1/3, and in females just over 1/3 of the maximum width of the eyestalk, these proportions being best seen by a view from the anterior aspect.

Antennules.—Peduncle very slightly shorter than the combined lengths of carapace and rostrum.

Antennae.—Basal segment together with proximal segment of exopodite equalling the length of the distal segment (scale), and reaching to the level of the anterior extremity of the eyes. Peduncle of endopodite nearly 1½ times the length of the antennal scale (excluding bristles) and about 1¼ times the anterior breadth of the carapace.

Mandibular palp.—Absent.

Rostrum.—Length about 60 per cent. of breadth, of a general triangular shape, with rounded anterolateral angles and nearly flattened apex.

Carapace.—Highly polished in fresh specimens, slightly dull after formalin fixation. Maximum breadth equalling the length (excluding rostrum) and being double the minimum breadth behind the anterolateral angles. Anterior borders between the rostrum and the anterolateral angles distinctly inclined posteriorly. Anterolateral angles with a well-developed spine directed slightly laterally. Lateral borders somewhat concave in their anterior third, then becoming convex and leading to the smoothly rounded posterolateral angles. Posterior borders smoothly concave.

Cervical groove distinct, gastric grooves distinct anterior to the cervical groove, and less so posteriorly. No trace of median, intermediate, or lateral carinae. Marginal carinae in the region anterior to the cervical groove not visible in males and just detectable in females. Posterior to the cervical groove the marginal carinae are distinct in both sexes and are best developed in their reflected portions. An inconspicuous pit is present in the mid line of the carapace about 1/3 of the way backwards from the anterior margin, and there is a conspicuous mid-dorsal tubercle just in front of the posterior margin of the carapace.

Raptorial claws.—Articulation of ischium and merus not terminal, but slightly in advance of the proximal end of the latter. Merus massive, with concave inferior margin. Upper margin of carpus carinated in 3 portions of which the distal portion is curved and low and leads to the middle portion with only a slight interruption. The middle portion ends abruptly in a blunt tooth and on the inner side near the middle there arises a tuft of setae. The proximal portion is erected as a single broad, blunt lobe. Propodus broad, shorter than the merus, and with a sinuous lower margin. Its upper margin is pectinate, with setae amongst the teeth and there are the usual 3 stout movable spines just inside the proximal part of the upper margin. Dactylus with 4 spines, the terminal one being much the longest. The lower margin of the dactylus curves smoothly.

Thoracic somites.—The fifth somite bears on each side a single short, spinous projection. The sixth, seventh, and eighth somites bear distinct intermediate carinae, and their lateral margins are carinate. There are no median or submedian carinae on the thoracic somites. The sixth and seventh somites have entire borders which are rounded and somewhat truncated posteriorly. Each lateral margin of the eighth somite bears a blunt ledge just anterior to the point of articulation of the appendages. Endopodites of the last 3 pairs of thoracic appendages are elongated ovoids.

Abdominal somites.—The first 5 somites bear distinct intermediate, lateral, and marginal carinae but median and submedian carinae are not present. On the sixth somite there are submedian, intermediate, lateral, and marginal carinae, the last 2 converging posteriorly. The following carinae end in spines; those bracketed not being present in some specimens, presumably owing to wear:

Carinae	Abdominal Somites
Submedian	6
Intermediate	5, 6
Lateral	(4), 5, (6)
Marginal	4, 5

The marginal carinae of the third abdominal somites end in a blunt point, barely conspicuous or sharp enough to be termed a spine.

Telson.—Broader than long and strongly convex. Median carinae very distinct and ending in a spine which is sometimes indistinct, presumably through wear. In unworn specimens a slight depression interrupts this carina about 1/5 of its length from the anterior end. Near the anterior border of the telson, in line with the submedian carinae of the last abdominal somite, there is a pair of tubercles. A row of tubercles, from 2 to 5 in number, lies on each side of the carina. These are not always symmetrically arranged on either side, and converge posteriorly to join in a small median tubercle just behind the median carina. Between these rows (referred to below as submedian tubercles) and the marginal teeth of the telson, there are in the males between 6 and 10 large tubercles.

These are arranged somewhat irregularly, but usually there is a marginal series and also an indistinct cluster near the anterior end of the line of submedian tubercles. In the females the equivalent tubercles are smaller and more numerous. There is an irregular group beginning in line with, and just outside, the anterior end of the submedian tubercle row. The remainder approximate to a series of lines which run from the marginal teeth to the centre of the anterior border of the telson. There are 5-7 lines present with about 5 tubercles in each. Between them the general surface of the telson is finely granular.

Submedian, intermediate, and lateral teeth of the telson (and also prelateral denticles) are present in a majority of specimens but in some the lateral teeth are absent or poorly developed on one side (e.g. left lateral in holotype, right lateral in allotype). In the males all the teeth are short, broad, and very inflated. They are normally smooth dorsally but in 2 specimens, less eroded than the remainder, the remains of tubercles are visible on their surfaces. The teeth are without spines in most specimens examined, but in some each ends in a spine, those on the submedian teeth being movable. In the females, these projections are longer, more pointed, and only slightly inflated. They are ornamented with a tuberculate carina or a short row of small tubercles some 4 or 5 in number, these rows merging into the general tuberculation lying medianly. The intermediate and lateral teeth end in sharp immovable spines, and the sockets corresponding to movable spines are present on the submedian teeth.

Denticles are distributed as follows on each side: submedian 2-4, typically 3, often worn and barely countable; intermediate, 7; lateral, 1 sometimes apparently worn away; also prelateral. The lateral borders of the intermediate teeth bear serrations of varying distinctions, usually obscure. Where the lateral tooth is missing there is either fusion of intermediate and lateral denticles as in the left side of the holotype (7 present); or, as in the right side of the allotype, this area bears an indeterminate number of serrations resembling those on the intermediate teeth.

The under surface of the telson is faintly granular, and there is a short but distinct post-anal carina.

Uropods.—The bifurcated process of the basal segment is armed internally with a variable number of teeth, usually 7-8, occasionally 6 or 9, with 2 of the teeth examined having bifid tips. The longer process is about thrice the length of the shorter and has a basal thickening on the margin facing the shorter process. The thickened region terminates abruptly and is curved concavely.

The external margin of the basal segment of the uropod bears 5-7 articulating spines, the terminal being much the largest. The terminal segment of the exopodite is approximately 2½ times as long as broad.

Colours.—These are described on specimens originally preserved for some weeks in formalin and then kept in alcohol. The latter effected no noticeable bleaching in a year.

Dorsally the general colour ranges from biscuit (Séguy 1936, 338-9) to dark ivory. The raptorial claws are ivory and the areas on the telson between the nodulations are sometimes pale slaty green (near Séguy 430), but generally pale blue-violet (near Séguy 555). The central area of the rostrum is a deep slaty blue (near Séguy 658) and the carapace is also faintly suffused with this colour. The carapace carries a distinct border of the same colour near its lateral margins and along most of its posterior border. The raised dorsal edge of the merus is also bordered by this colour, which is continued posteriorly as an irregular reticulation. Near the posterior margins of the free thoracic somites and of the first 5 abdominal somites, there are conspicuous dark lines. In pale specimens these are sooty black; in dark specimens they are dark brown (Séguy 642) fading at the edges to dull violet-brown (Séguy 643).

The ventral surface is slightly lighter than the dorsal. The fringes of the uropods are a dull orange (near Séguy 203) as are the hairs on the last segment of each thoracic appendage (excluding raptorial claw).

There is no black pigment on the uropods.

Discussion

The present species belongs to the "*Chloridella*" group of the genus (Miers 1880; Tweedie 1935). This group now comprises the following species: *S. microphthalma* H. M. Edwards 1837; *S. latreilli* (Eydoux & Souleyet 1841); *S. decorata* (Wood-Mason 1875); *S. depressa* (Miers 1880) Serène 1952; *S. rotundicauda* (Miers 1880); *S. chlorida* Brooks 1886; *S. gibba* Nobili 1903; *S. choprai* Tweedie 1935; and *S. granti,* the present species.

The group is characterized throughout by the possession of short, broad eyestalks which are wider than the cornea. Some species are known to have the ischio-meral articulation of the raptorial claws in advance of the proximal end of the merus (*S. choprai*, *S. granti,* and *S. depressa* as examined by the present writer). In other species this feature has apparently not been looked for. Re-examinations are desirable because in this respect the group as a whole might not conform to the accepted diagnosis of the genus (Kemp 1913), as Tweedie (1935) has pointed out in relation to *S. choprai.*

In most species of the group the carinae on the carapace are poorly developed, with only the reflexed portions of the marginals being at all distinct. This does not apply to *S. gibba* and may or may not apply to *S. rotundicauda* and *S. chlorida.* It is important for the remainder, because, while there is agreement with Kemp's diagnosis of the genus: "longitudinal carinae [of the carapace] usually distinct, never wholly absent", there is a possibility of confusion in operating his key in which the prime feature of the genus is given as: "Carapace with well marked carinae".

Another feature of several representatives of the group is the marked sexual dimorphism in the structure of the telson. The males have broad and inflated teeth, whereas in the females the teeth are sharper and ornamented with small tubercles linearly arranged. This applies to *S. latreilli* (Kemp 1913), to *S. depressa* (Serène 1952), to the present species, and possibly to others (Serène 1952).

Amongst the various members of this "*Chloridella*" group of species, *S. granti* appears to most nearly resemble *S. depressa* and *S. choprai*. It is readily distinguishable from both by the absence of a mandibular palp and by the different nature of the keel on the dorsal side of the raptorial carpus.

In Figure 2*D* this keel is shown, with comparable figures for a paratype of *S. choprai* and a Queensland specimen of *S. depressa* (Figs. 2*C* and *E* respectively).

SQUILLA TERRAREGINENSIS, sp. nov.

Fig. 3*A*, *B*

Material

Holotype.—♂, 92 mm., near mouth of Barron R., Cairns, Queensland, presented to Australian Museum, May 1928, by G. A. V. Stanley.

Allotype.—♀, 54 mm., Cooktown, Queensland, presented to Australian Museum, Aug. 1913, by A. R. McCulloch.

Paratypes.—*Males*, 75 mm., details as allotype; 88 mm., Barron R., Cairns, Queensland, 25.viii.1952, per Mr. D. J. Tranter to University of Queensland (sweep net in small brackish tributary near mouth Barron R.) (Queensland Museum).

Diagnosis

Very similar to *S. scorpio* Latreille 1825, but differing from it in possessing a shorter rostrum somewhat resembling *S. scorpio* var. *immaculata* Kemp 1913. It differs from both Latreille's species and Kemp's variety in possessing a mandibular palp, in having a pointed tip to the ophthalmic somite, and in the distribution of spines on the carinae of the abdominal somites.

Description

Eyes.—Eyestalks short and broad, the breadth of the cornea equalling the length of the stalk and being about 2/3 of the breadth of the stalk before it widens to the cornea. The cornea is set obliquely on the stalk and the ophthalmic somite terminates anteriorly in a distinct point (Fig. 3*A*).

Antennules.—Peduncle short, 2/3 of the length of the carapace (excluding rostrum).

Antennae.—Basal segment together with proximal segment of exopodite equalling 2/3 of the length of the distal segment (scale). Peduncle of endopodite short, about $\frac{1}{2}$ the length of the antennal scale (excluding bristles), about 60 per cent. of the anterior breadth of the carapace, and reaching just to the level of the front of the cornea.

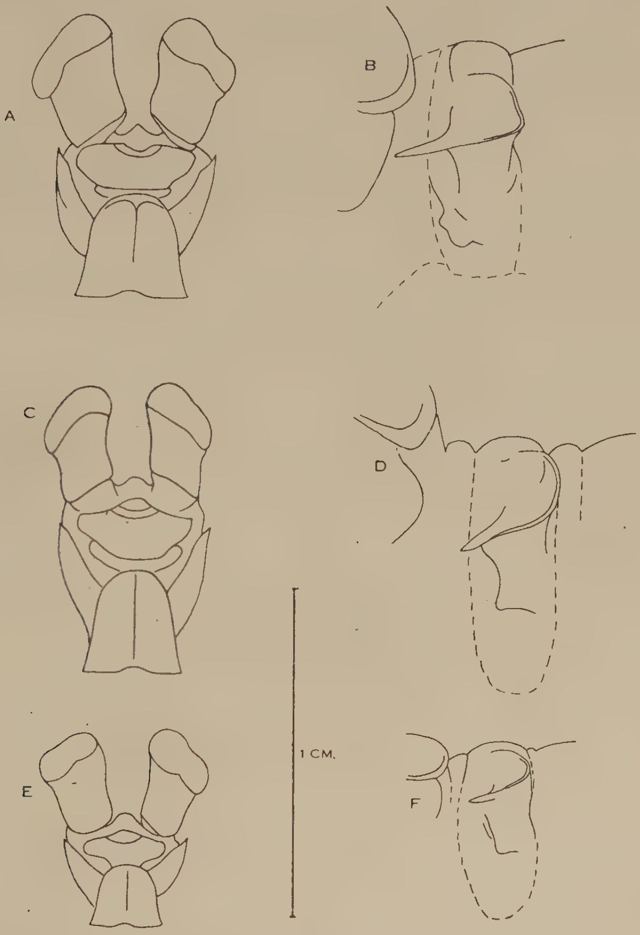

Fig. 3.—*A*, Dorsal view of rostrum, antennular somite, and ophthalmic somite of holotype, of *S. terrareginensis*, sp. nov.
B, Lateral view from the left of the fifth thoracic somite of above holotype to show the falcate lateral process and protrusions beneath it.
C, View as *A*, 90 mm. male *S. scorpio* (from Fish-market, Singapore).
D, View as *B*, specimen as *C*.
E, View as *A*, 60 mm. male *S. immaculata* (from Muer, Johore).
F, View as *B*, specimen as *C*.

Mandibular palp.—Present. In situ only 2 segments are distinguishable.

Rostrum.—Maximum length equalling maximum breadth, tongue-shaped, with a sharp and distinct median carina in its distal half.

Carapace.—Highly polished. The maximum breadth is 3/4 of the length, which in turn is double the minimum breadth behind the anterolateral angles. These angles bear strong spines, which just fail to reach the level of the rostral base because of the posterior inclination of the margins lateral to the rostrum. Ventral to each anterolateral spine a subacute lobe is situated. Lateral borders of the carapace straight, posterolateral margins rounded.

Cervical and gastric grooves distinct. Median carinae distinct in front of the cervical groove but obsolete anteriorly, and bearing a small median dorsal pit near its middle. Intermediate carinae well marked; lateral carinae well developed anteriorly and posteriorly but less so (though distinguishable) in the middle. Marginal carinae distinguishable throughout their length, but only conspicuous in the posterior reflected portions. The posterior margin of the carapace between the gastric grooves has a thickened edge, and from its centre a short median keel runs forwards from a conspicuous tubercle.

Raptorial claws.—Outer inferior margin of the merus bluntly rounded anteriorly. The carpus, which has the usual groove on its outer side, bears an entire dorsal carina which terminates acutely before reaching the distal margin. In the single female available the distal end of the propodus is not distinctly broader than in the males. Dactylus with 5 teeth, including the apical one, with a small proximal lobe, and with a sinuous lower border.

Thoracic somites.—The fifth somite bears a pair of broad, blunt inferior protrusions of characteristic bilobed shape (Fig. 3*B*). The single lateral lobe consists of a strong falcate process ending in a sharp, forwardly directed spine. The carina equivalent to the intermediate carina of this somite is directed obliquely to continue as a thickening of the posterior margin of the falcate spine. The anterior margin of the fifth somite is thickened into a distinct ridge.

The sixth, seventh, and eighth somites bear distinct submedian and very well-developed intermediate carinae. The lateral margins of the sixth and seventh somites are rounded; the eighth bears a blunt anterior lobe.

Abdominal somites.—The first 5 bear 4 distinct pairs of longitudinal carinae, the submedians of the second somite being interrupted about 1/3 of their distance from the front in the position of a transverse pigmented area. On the sixth somite the marginal carinae are indistinct and the submedian are swollen in the male. The following carinae end in spines;

those bracketed not being present in some individuals, presumably owing to wear:

Carinae	Abdominal Somites
Submedian	6
Intermediate	5, 6
Lateral	(4), 5, 6
Marginal	(1), 2, 3, 4, 5

Telson.—Slightly broader than long. Median carina well marked and terminating in a small spine overhanging a blunt tubercle. This carina is sharply ridged in the female and broadly rounded in the male, particularly in its posterior half. There is a small pit on the median carina about 1/6 of its length from the anterior end. On either side of the carina the telson appears smooth to the naked eye, apart from traces of symmetrically arranged shallow pits. Under a lens the surface is finely rugose.

Lateral, intermediate, and submedian teeth are present, each forming the termination of a short carina. The carinae are broader and rounder in the males than in the female. Denticles on each side are distributed as follows: submedian, 2 or 1; intermediate, 4 or 5; lateral, 1; also prelateral.

The under surface of the telson is smooth to the naked eye, but finely rugose under a lens. It bears a series of symmetrically arranged shallow pits, the only conspicuous ones being a paired row on either side of the midline directed towards the submedian teeth.

Uropods.—The bifurcated process of the basal segment is finely serrated internally. The inner spine, which is about thrice the length of the outer, bears a prominent external lobe beyond its mid point, and is strongly concave in the portion proximal to the lobe. The basal segment of the exopodite bears on its external margin either 6 or 7 articulating spines, the terminal being much the largest. The terminal exopodite segment is twice as long as broad.

Colours.—After prolonged alcohol preservation the only noteworthy colours are indistinct dusky patches on (*a*) the lateral processes of the fifth thoracic somites, (*b*) the second abdominal somite as a transverse band, and (*c*) the distal end of the basal segment of the exopodite of the uropod.

In a male specimen kept for a month in formalin and another month in alcohol, colours are as follows: The general dorsal surface is greenish buff with numerous small dark chromatophores. The greenish pigmentation becomes more distinct in the telson, particularly on the carinae, which are olive green (Séguy 206). The chromatophores are especially conspicuous as individual dots on the peduncle of the antennule, and are concentrated to form dusky transverse marks at the posterior edges of the carapace and all the free thoracic and abdominal segments except the first and the last. There are similar dusky patches in the mid-dorsal regions of the third, fourth, and fifth abdominal somites, and also the transverse bar (already mentioned) in the second abdominal somite. The cornea, lateral processes of fifth thoracic somite, and the distal end of the basal exopodite segment of the uropod are all deep black. The following areas are tinged with reddish brown (Séguy 173): median carina of carapace, mid-dorsal tubercle and carina on the posterior end of the carapace, submedian and intermediate carina of the sixth abdominal somite. The ventral surface is cream-coloured except for the telson, which has an olive-green tinge becoming conspicuous distally. The inner surface of the raptorial merus bears violet-blue markings (Séguy 549).

Discussion

The species is so strikingly similar to *S. scorpio* that separate figuring of the general facies is unnecessary. It is extremely likely that its novelty would pass unnoticed without an examination of the mandibular area. It is possible that some records of the occurrence of *S. scorpio*, and particularly Miers' (1880) from Port Essington in North Australia, refer to the present species.

The main diagnostic features have already been summarized. The differences in the shape of the ophthalmic somite are shown in Figure 3*A, C, E*, which shows the present species and specimens of *S. scorpio* and its variety *immaculata* respectively. To these differences one might add the shapes of the lobes lying beneath the fifth thoracic somite (Fig. 3*B, D, F*). Kemp (1913, p. 43) describes these as "broad tooth-like lobes" in *S. scorpio* and this applied accurately to specimens received from the Raffles Museum. In the present species the processes are broader, blunter, and bilobed.

It is also possible that the colours of fresh specimens might serve for distinction, but this must remain uncertain until more and fresher specimens of the present species come to hand.

In several respects *S. terrareginensis* is intermediate between *S. scorpio* and Kemp's var. *immaculata*. These concern firstly the shape of the rostrum, secondly the distinctness of the lateral carinae of the carapace, and thirdly the distinctness of the black patch on the lateral processes of the fifth thoracic somite after prolonged preservation. In the present species it fades more rapidly than the remaining black marks, and eventually becomes very faintly recognizable.

The marked similarity of *S. terrareginensis* to *S. scorpio* shows that in this particular section of the genus specific distinctions depend upon a small number of characters. It is likely that other species in this section will be characterized in a similar fashion by very few features. *S. scorpio* var. *immaculata* is distinguished from *S. scorpio* by only 5 such features, but they appear to be distinctive and in two instances resemble characters of the present species. Kemp (1913, p. 45) has further noted that there appears to be ecological separation between *S. scorpio* and its variety.

The case for elevation of *S. scorpio* var. *immaculata* to specific rank as *S. immaculata* Kemp is a strong one.

SQUILLA MCNEILLI, sp. nov.

Fig. 4*A-F*

1900 *Squilla armata* Whitelegge, T. "Crustacea I" Mem. Aust. Mus. IV, p. 199,

Material

All contained in the collections of the Australian Museum and all from New South Wales localities.

Holotype.—♀, 86 mm., off coast between Merimbula and Tathra, about 40 fathoms.

Allotype.—♂, 71 mm., off Wata Moli near Botany Bay, 68 fathoms, 7.ii.1919 (trawled).

Paratypes.—Only the starred specimens were at hand in writing the final description. *Females.* 73 mm.,* "Thetis" Stn. 8 off Broken Bay, 25-28 fathoms (labelled, presumably by Whitelegge, "*Squilla armata* M. Edw., Station 8;" and by McNeill "*Squilla* (sp. indet.) = *Squilla armata* Whitelegge nec. authors"); 78 mm.,* 3-4 miles off Eden, 25-30 fathoms, A. Livingston and H. Fletcher (from stomach of "flathead"); 44 and 54 mm., Newcastle district (seine trawler); 64 and 80 mm., other data as allotype; 54 mm., 8 miles S. Green Cape, 30 fathoms, 20.vii.1925, M. Boardman (trawled); 41 mm., 11-12 miles NE. Port Jackson, about 75 fathoms, M. Ward (from stomach of trawled specimen of *Halientaea brevicauda*); 53 mm., off coast between Botany and Jervis Bays, early Jan. 1943, G. P. Whitley (from stomach of trawled gummy shark, *Emissola antarctica*); 66 mm., off coast between Botany and Jervis Bays (from stomach gummy shark).

Males, 68 mm.,* 7 miles N. of Twofold Bay, 40-45 fathoms (trawled); 73 mm., off Botany Bay, deep water, Oct. 1924, M. Ward (from deck and nets of Trawler "Thistle" in port); 71 mm., NNE. of Montague I., 90 fathoms (Trawler "Gunner"); 40, 58, and 76 mm., off Botany Bay, 33-56 fathoms, Aug. 1921, F. A. McNeill and A. Livingstone (from stomach of trawled shark); 49 and 65 mm., off Port Hacking, 40-50 fathoms, A. Ward; 61 mm., 12-22 miles NE. from Green Cape, 39-46 fathoms, June 1924, A. Livingston and H. Fletcher; 78 and 85 mm., other data as holotype; 45 and 50 mm., off Jervis Bay, 30-40 fathoms, 22-29.xii.1942, G. P. Whitley (from stomach of trawled gummy shark, *Emissola antarctica*); 81 mm., off Botany Bay, 55-60 fathoms, A. G. Flet (trawled); 66 mm., June 1943 (from stomach of trawled gummy shark).

Summation of above.—16 males, lengths 40-81 mm., 13 females, lengths 41-86 mm. Mostly trawled off the New South Wales coast at depths from 25 to 90 fathoms; this being an unusually great depth for a stomatopod. Several from stomachs of trawled fish (especially sharks).

Diagnosis

Characterized by an arrow-head shaped rostrum, long telsonic teeth, long mandibular palps, and by the lateral and marginal carinae of all the abdominal somites ending in spines. In many other respects showing resemblances to the *S. scorpio*, *S. immaculata*, and *S. terrareginensis* groups of the genus.

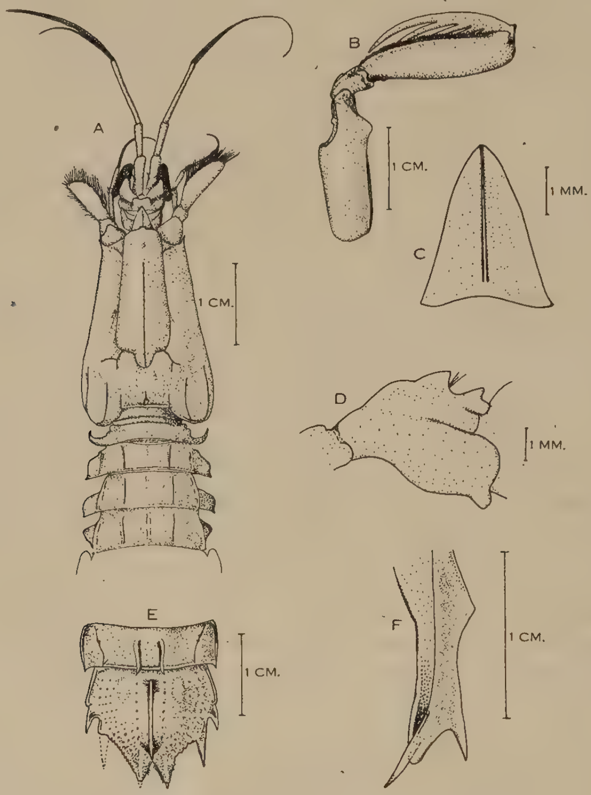

Fig. 4.—*Squilla mcneilli*, sp. nov., holotype.
A, Dorsal view of anterior half of body.
B, External view of right raptorial claw.
C, Dorsal view of rostrum.
D, External view of right raptorial dactylus.
E, Ventral view of bifurcated process of left uropod.

Named after Mr. F. A. McNeill in token of friendship and his early cognizance of the novelty of the species.

Description

Eyes.—Eyestalks short and diverging. Cornea set very obliquely on the stalk, its greatest length about double that of the eyestalk (less cornea). The anterior termination of the ophthalmic somite is flattened.

Antennules.—Long; the peduncle is 9/10 the length of the carapace excluding rostrum, and the entire appendage just over $1\frac{1}{2}$ times this length. The dorsolateral processes of the antennular segment of the head are produced into sharp spines pointing in an anterodorsal direction.

Antennae.—Basal segment plus proximal segment of exopodite short, not reaching to the tip of the rostrum, and only 2/5 the length of the distal segment (scale). The latter is long and narrow, the length being 5 times the breadth. Peduncle of endopodite short, about 2/3 the anterior breadth of the carapace and not reaching to the level of the front of the cornea.

Mandibular palp.—Three-segmented, very long, about $\frac{1}{2}$ the anterior breadth of the carapace.

Rostrum.—Distinctly longer than broad, arrow-head shaped, with the sides of the basal $\frac{1}{2}$ straight, and the distal $\frac{1}{2}$ curving slightly to the acute tip. It bears an elevated median carina running from just in front of its posterior margin to the anterior tip.

Carapace.—Polished, elongated, with maximum breadth 2/3 of the length, which in turn is distinctly more than double the minimum breadth behind the anterolateral angles. These angles have long, acute spines which just fail to reach the level of the rostral base. Anterolateral borders inclined posteriorly and concavely curved to the point of origin of the anterolateral spines. Lateral borders straight to the level of the cervical groove.

Cervical and gastric grooves distinct. Median carina distinct in front of the cervical groove but obsolete anteriorly and bearing a small median pit about 1/3 of its length from the front. In the mid line just behind the level of the bases of the anterolateral spines there is a large, shallow depression. Intermediate carinae conspicuous posterior to the level of the cervical groove; anterior to this level they are only indicated by a broad, rounded longitudinal elevation. Marginal carinae only visible in the posterior 1/5 of the carapace where they are conspicuously elevated, and remaining so in the anterior reflexed positions. There is a mid-dorsal tubercle and short median carina just in front of the posterior margin of the carapace.

Raptorial claws.—Outer inferior margin of the merus obtusely rounded anteriorly. Carpus with a dorsal carina terminating in a blunt tooth and then an acute anterior tooth distinctly separated from it. In this space, just in front of the carina, is a small tuft of setae. Propodus long, narrow, and thin. Dactylus with 5 long, slender teeth (including the apical tooth). Its lower border bears a small proximal lobe and thereafter follows a smoothly convex curvature.

Thoracic somites.—Each lateral lobe of the fifth somite consists of a fairly slender falcate process terminating in a sharp, forwardly directed spine. The intermediate carina of this somite curves laterally and runs near the posterior margin but is not continued on to the falcate process.

The anterior margin of the fifth somite is thickened into a distinct ridge.

The sixth, seventh, and eighth somites bear well-developed submedian and intermediate carinae, while the seventh carries a faint and the eighth a distinct median carina. The lateral margins of the sixth and seventh somites are acutely pointed and terminate in backwardly directed spines, while the eighth bears a stout, outwardly directed, and right-angled process.

Abdominal somites.—The first 5 bear distinct median, submedian, intermediate, lateral, and marginal carinae. The medians of each somite except the first are interrupted and form 2 more or less distinct carinae, one in front of the other. The laterals on the second somite are similarly interrupted, and indistinct interruptions (best seen in lateral view) are visible on intermediate carinae of all excepting the first somite. The sixth somite has no median carina but the other carinae are very distinct and equally sharp and elevated in both sexes. The laterals and marginals converge in the usual fashion, and the intermediates bear indistinct tubercles near their centres. The following carinae end in spines:

Carinae	Abdominal Somites	
Submedian	6	
Intermediate	2, 3, 4, 5, 6	
Lateral	1, 2, 3, 4, 5	6
Marginal	1, 2, 3, 4, 5	

Telson.—Slightly broader than long. Median carina very acute and ending in a sharp spine overhanging a tubercle. There is a slight interruption about 1/6 of its length from the anterior end. In the anterior ½ of each side of the telson, about midway between the carina and the margin there is a broad, low ridge with flat, irregular, polished tubercles. The remainder of the telson surface bears lines of shallow pits upon a general surface which is rugose in unworn specimens. The pits are in 2 series: (*a*) about 8 pairs in a submedian position at the sides of the median crest and (*b*) about 14 lines on each side, arising near the margins, converging as towards the centre of the telson, these pits being slightly smaller than those of the previous series.

The prelateral area is carinate and ends in a blunt lobe. Lateral, intermediate, and submedian teeth are present and the area between the submedians is deeply indented. The lateral teeth are moderately long and end in sharp spines, the intermediates are extremely long, reaching to or just beyond the level of the end of the telson in the midline and also end in sharp spines. The submedian teeth, which carry carinae, are long and end in articulating spines. Denticles on each side are distributed as follows: submedian 14-17; intermediate 8-10; lateral 1; also prelateral lobe.

The under surface of the telson bears a broad post-anal elevation barely distinct enough to be termed a carina and on either side there are numerous series of shallow pits whose distinctness is reduced with wear.

Uropods.—The bifurcated process of the basal segment is finely serrated internally. The inner lobe, which is about twice the length of the outer, bears a very prominent external lobe beyond its mid point and is strongly concave in the proximal portion. The basal segment of the exopodite bears on its external margin either 7 or 8 articulating spines, the terminal being much the largest. The terminal exopodite segment is just less than twice as long as broad.

Colours.—Most specimens after prolonged alcohol preservation are reduced to the usual biscuit colour, with traces of darker pigment. The holotype shows the pigmentation better than any other specimens, and has dusky areas as follows: near the posterior margins of first, fourth, and sixth abdominal somites; just outside and in line with the submedian carinae of the first 4 abdominal somites and the intermediate carinae of the first 5 abdominal somites; just inside the submedian carinae and between the lateral and marginal carinae of the sixth abdominal somite; round the anterior and especially the posterior origins of the median carina of the telson, and also marking the shallow marginal pits on its dorsal surface. In addition the uropod bears pigment as follows: on the upper external portion of the basal segment; down the internal side of the ventral face of the basal process; at the distal edge of the proximal segment of the exopodite and down the centre of the distal segment; and as a central line, widening posteriorly, on the endopodite.

Discussion

The novelty of the present species has been known for many years by Mr. F. A. McNeill, by Dr. Tweedie of the Raffles Museum (who left notes to this effect at the Australian Museum), and by Dakin and Colefax (1940) who state as follows in relation to New South Wales stomatopods: " . . . another very common form which is brought in by the trawlers remains still indetermined." It is fortunate that Whitelegge's type is retained by the Australian Museum so that his mistaken determination can be rectified.

S. mcneilli is unique in certain of its characters, and in others exhibits a unique combination of characters. The telson shows resemblances to those of *S. leptosquilla* Brooks 1886 and *S. tenuispinis* Wood-Mason 1891 but has not such an extreme development of the intermediate teeth. The present species also differs conspicuously in having 5 spines on each raptorial dactylus and in possessing mandibular palps.

The presence of a median carina on the carapace, the 5 teeth on the raptorial dactylus, the falcate process on the margins of the fifth thoracic somites, and the structure of the basal bifurcated process of the uropods all tend to relate the species to the *S. scorpio*, *S. immaculata*, and *S. terrareginensis* group, and especially to the last species, which possesses a mandibular palp. The marked dissimilarities in the structure of the telson indicate, however, that the relation is anything but close, and this is further emphasized by such unique characters as the shape of the rostrum, the length of the mandibular palp, and the distribution of spines on the abdominal somites.

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AERIAL OBSERVATIONS ON THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), WITH NOTES ON OTHER SPECIES

By R. G. Chittleborough*

(*Manuscript received May 27, 1953*)

Summary

Aerial observations of humpback whales in the region of Point Cloates, Western Australia, during 1952 are recorded. The first southward-moving humpback whale was sighted on July 21, while decreasing numbers were seen moving northwards until early October. In 1952 the change from a predominantly northward migration of humpback whales to a southward migration occurred close to August 24. The speed of migration of a number of these whales is recorded, the mean value being 4.3 kt. A few humpback whale calves were sighted early in July and a peak in their occurrence in August suggests maximum frequency of parturition early in August. A very great increase in the occurrence of calves in the area late in the season suggests that female humpback whales rearing calves move southwards later than other individuals. Some evidence is presented that Exmouth Gulf is a nursery area.

The presence of some killer, fin, blue, and minke whales in the area is noted.

I. Introduction

The Norwest Whaling Company, operating from a shore station at Point Cloates on the Western Australian coast, engages a pilot flying an Auster aircraft for the purpose of locating suitable humpback whales to be taken by the catching vessels.

Under normal conditions at an altitude of 800-1000 ft it is possible to distinguish not only the species of whale and whether a calf is present but also, after some experience, whether a humpback whale is large enough to be taken by the catching vessels.

From July to early October 1952, by the ready cooperation of Mr. J. F. Pekin, the pilot of the aircraft, numerous aerial observations were made on whales and their movements in the region of Point Cloates. The author accompanied the pilot on a number of the flights.

The observations obtained are recorded and discussed in the present report. Most of the records are on the humpback whale (*Megaptera nodosa* Bonnaterre) and concern the direction and speed of migration, the presence of new-born calves, and the possibility that Exmouth Gulf is a "nursery" area for the species.

The aerial photographs of humpback whales used in this report were taken some years ago off the West Australian coast by an officer of this Division, Mr. S. Fowler, while engaged upon fisheries exploration flights.

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From a large number of photographs then obtained, these have been selected as showing typically the appearances upon which the facts presented in this paper are based. The photographs were taken at lower altitudes than those maintained during the flights when the present observations were made.

II. HUMPBACK WHALES

(*a*) *Direction of Migration*

In order to find the time when the migration of the humpback whales in the area changed from a northward to a southward movement, a record was made as often as possible of the direction of movement of whales sighted from the aircraft. This was noted for 560 humpbacks in the neighbourhood of Point Cloates between June and October 1952. In almost every case the direction was within a few degrees of north or south.

TABLE 1

HUMPBACK WHALES OFF POINT CLOATES: DIRECTION OF MIGRATION

Seven-Day Period Ending	Moving North		Moving South	
	Number	Percentage	Number	Percentage
8.viii.52	12	92.3	1	7.7
15.viii.52	21	75.0	7	25.0
22.viii.52	58	81.7	13	18.3
29.viii.52	61	43.0	81	57.0
5.ix.52	11	21.2	41	78.8
12.ix.52	15	22.7	51	77.3
19.ix.52	8	10.7	67	89.3
26.ix.52	3	7.9	35	92.1
3.x.52	1	2.6	38	97.4
10.x.52	1	2.7	36	97.3

In June and July almost every humpback whale observed from the air was moving northwards. Towards the end of July the first southward-moving humpbacks were sighted, the first one on July 21, and two more on July 30. From the beginning of August southward-moving humpbacks were seen with increasing frequency.

In Table 1 the proportions moving north and south are shown for weekly periods from August to early October. The weekly totals do not indicate the total number of humpback whales sighted, as whales were often seen to blow too far distant to observe the direction they were travelling, and these could not always be examined as nearer whales were under observation at the time. However, the series shown in Table 1 may be regarded as a random sample.

From Table 1 the curves in Figure 1 have been drawn to indicate the trends in humpback whale movements off Point Cloates in 1952. This figure shows that the change from a predominantly northward migration to a southward one occurred close to August 24, but that this change was not abrupt. There were still occasional humpback whales moving northwards early in October. One whale observed from the air moving northwards near Point Cloates on October 1, 1951, was a large, very rotund individual travelling alone and was considered by the pilot to be a female in late pregnancy.

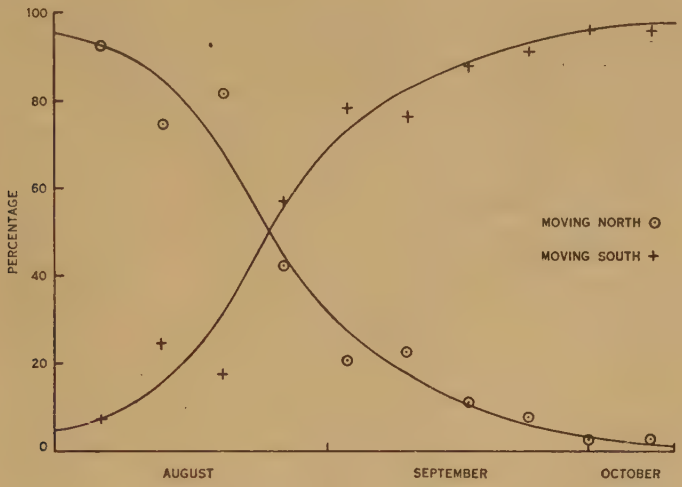

Fig. 1.—Humpback whales off Point Cloates, 1952. Proportions moving north and south.

In his account of earlier operations at Point Cloates Dakin (1934) refers to the time of onset of the southerly migration. He observes (p. 176) that off Point Cloates in 1912 the humpback whales began returning south about August 24, while in 1913 (p. 195) the southward movement began early in August, reaching its peak by August 17.

Although the time of change from northward to southward migration might vary a little from year to year, the observations made in 1952 show that this change is spread over 10 wk and that in 1952 equal numbers were moving northward and southward close to August 24 (Fig. 1).

(*b*) *Humpback Whale Speeds*

As far as can be ascertained, no records have previously been published of the speeds at which humpback whales swim in the undisturbed state. It is generally accepted that they travel at a slower rate than other species such as fin and blue whales. Gunther (1949) states that fin whales (*Balaenoptera physalus* Linné) at times keep abreast of a ship travelling at 10-12 kt and occasionally travel for short distances at an estimated 16-18 kt. However, these whales were not on an undisturbed migration.

In the region of Point Cloates it was possible at times to fix the position of a selected humpback whale or group observed from the air and to check the position of the same whale or group some hours later. From such records the speeds of migration of these humpback whales were calculated, with the results shown in Table 2.

The records are separated into two series, those where a calf was present and those without calves. Generally a whale with a calf travelled more slowly than whales without a calf. In two cases the calf had only recently been born, as indicated by its very light colour and small size (Plate 1, Fig. 1). In both cases the cow and young calf were travelling slowly, at average speeds of 2.8 and 3.5 kt respectively. It has been found by the author that near-term foetuses always have very lightly pigmented skin, this character persisting for a short time after birth. As the calf grows it darkens as shown in Plate 1, Figure 2. Such cow and calf pairs then travel slightly faster. The average speed of the humpback whales in Table 2 was 4.3 kt.

TABLE 2

HUMPBACK WHALE SPEEDS, POINT CLOATES

Date Observed	Type of Group	Times Observed From	Times Observed To	Total Hours	Nautical Miles Travelled	Direction	Speed (kt)
15.viii.52	3 Cow-calf pairs*	0800	1230	4.5	11.5	N	2.6
10.ix.52	Cow-very young calf	1030	1140	1.17	3.3	N	2.8
6.x.51	Cow-calf	1350	—	—	—	—	3.0
6.x.51	2 Adults-1 calf	1345	1615	2.5	7.5	—	3.0
29.viii.52	2 Adults-1 calf	0735	1015	2.67	8	N	3.0
18.viii.52	Cow-calf	0815	1100	2.75	9	N	3.3
21.vii.52	Cow-very young calf	0930	1100	1.5	5	N	3.3
		1100	1515	4.25	15.25	N	3.6
		0930	1515	5.75	20.25	N	3.5
28.viii.52	Cow-calf	0730	1030	3	11	N	3.7
27.vii.52	Cow-calf	0855	1210	3.25	12.5	N	3.85
14.vii.52	Cow-calf	0955	1210	2.25	9	N	4.0
		1210	1520	3.17	12	N	3.8
		0955	1520	5.42	21	N	3.9
11.x.51	Cow-calf	0800	1515	7.25	32	S	4.4
1.ix.52	Cow-calf	1000	1040	0.67	3	N	4.5
15.vii.52	Cow-calf	1550	1700	1.17	6	N	5.15
7.viii.52	Cow-calf	1020	1210	1.83	11.8	N	6.4
6.viii.52	Cow-calf	0800	1130	3.5	27	N	7.7
3.viii.52	2 Adults	1130	1555	4.42	16	N	3.6
30.vii.52	2 Adults	0930	1015	0.75	3.2	N	4.26
16.vii.52	3 Adults	0950	1430	4.67	20	N	4.3
15.vii.52	1 Adult (large)	0845	1045	2.0	10.75	N	5.4
11.vii.52	1 Adult	1215	1535	3.33	19	N	5.7
17.vii.52	1 Adult	0915	1020	1.08	7	N	6.5

* Three pairs from ½ to 1½ miles apart; maintained their relative positions over 4½ hr.

(*c*) *Presence of Calves amongst Humpback Whales off Point Cloates*

A record was kept of humpback calves sighted from the aircraft. Usually a calf accompanied a single adult, but sometimes two adults were present. The dates on which the first calves were seen and when the proportion of calves in the sightings first rose considerably should give further evidence on the time of parturition. To this end, the total numbers of calves observed in weekly periods were expressed as percentages of the weekly total numbers of adult humpbacks observed sufficiently closely to establish whether or not a calf was present. These weekly totals and percentages are shown in Table 3 and the percentages graphed in Figure 2.

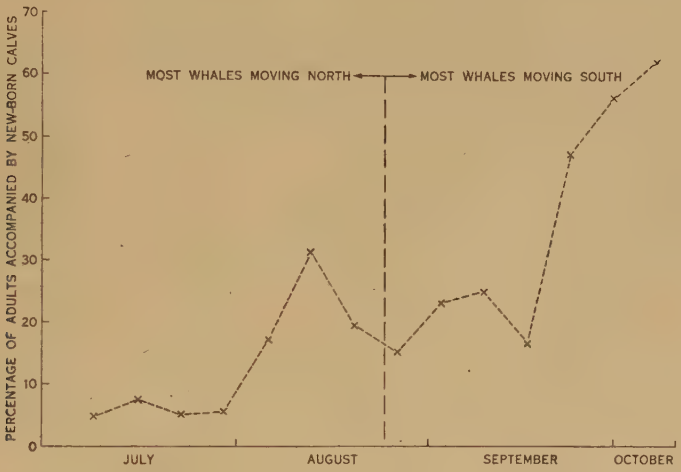

Fig. 2.—Occurrence of humpback whales off Point Cloates, 1952.

A small proportion of calves was present early in July at the commencement of the aerial observations. From this it would seem that parturition in a few cases must have taken place late in June or even earlier.

In August calves were of relatively common occurrence, as shown in Figure 2, the peak in the second week suggesting a high frequency of births early in August. This confirms Matthews's (1937) conclusion, based on a consideration of foetal lengths, that in the humpback whale maximum frequency of parturition occurred in August.

In late August and the first half of September, when the majority of humpback whales were moving south (Fig. 1), the proportion of calves remained relatively constant; but in late September and early October the proportion of calves amongst the humpback whales observed off Point Cloates greatly increased (Fig. 2). Almost all the calves then seen were much darker and slightly larger than those seen shortly after birth. The very high rise in the proportion of these calves late in the season suggests that the majority of cows rearing calves begin their southward migration later than other individuals.

(*d*) *Humpback Whales in Exmouth Gulf*

Exmouth Gulf is a large, relatively shallow gulf a few miles north of Point Cloates. While whale-spotting during the 1951 catching season, Mr. J. Pekin noted that in September there were large numbers of adult humpback whales with calves in this gulf, indicating that it was a nursery area for this species. It was hoped that in 1952 aerial surveys could be made of this gulf at intervals through the winter and spring, but no such flights could be made until late September. The results of three surveys are summarized in Table 4.

TABLE 3

PROPORTIONS OF CALVES AMONGST THE MORE CLOSELY OBSERVED HUMPBACK WHALES OFF POINT CLOATES

Seven-Day Period Ending	Total Adults Checked for Calves	Calves Sighted	
		Number	Percentage
11.vii.52	41	2	4.9
18.vii.52	122	9	7.4
25.vii.52	100	5	5.0
1.viii.52	69	4	5.8
8.viii.52	75	13	17.3
15.viii.52	64	20	31.3
22.viii.52	72	14	19.4
29.viii.52	79	12	15.2
5.ix.52	52	12	23.1
12.ix.52	56	14	25.0
19.ix.52	48	8	16.7
26.ix.52	40	19	47.5
3.x.52	39	22	56.4
10.x.52	37	23	62.2

TABLE 4

AERIAL SURVEYS OF HUMPBACK WHALES IN EXMOUTH GULF, 1952

Date	Humpback Whales Sighted				Percentage of Adults with Calves
	Single Adults	Cow-calf Pairs	Adult Pairs	Groups of 3 Adults	
24.ix.52	—	17	6	1	53
30.ix.52	—	8	—	—	100
9.x.52	—	17	3	—	74

While Table 4 shows that a high proportion of the humpback whales in this gulf were accompanied by calves, these surveys were made too late in the season to show that large numbers of females gather here when rearing calves.

III. OTHER SPECIES OF WHALES IN THE REGION OF POINT CLOATES

(*a*) *Killer Whales* (Orcinus orca *Linné*)

Schools of this species were sighted on a number of occasions off Point Cloates during 1952. The records are summarized in Table 5.

TABLE 5

KILLER WHALES SIGHTED OFF POINT CLOATES IN 1952

Date	Number	Direction	Remarks
17.viii.52	5	S	—
24.viii.52	*c.* 50-60	S	Amongst a stream of southward-moving humpbacks which appeared to be changing direction more than usual
	Several	N	Close to six humpbacks moving south
9.ix.52	*c.* 40	S	Close to three adult humpbacks moving south
11.ix.52	Over 30	—	Appeared to be coming in from west, closing in on several humpbacks

In addition to these, large numbers of killer whales, estimated by Mr. J. Pekin as at least 150, were seen in Exmouth Gulf during a survey flight on September 24. Apart from hunting by man, the mortality rate amongst humpback whales is probably highest immediately after birth and at this stage killer whales may make successful attacks. In October 1951, Mr. J. Pekin observed in Exmouth Gulf four or five killer whales attacking a group of humpback whales consisting of two adults and a calf. One adult humpback (presumably the cow) kept the calf very close, while the other adult (possibly a bull) charged the killer whales, beating them off with its flukes. A very similar incident occurred off Point Cloates in the 1952

TABLE 6

FIN AND BLUE WHALES OBSERVED OFF POINT CLOATES, 1952

Date	Species	Number	Distance Off Shore (miles)	Direction	Remarks
12.ix.52	Blue	1	5	S	—
17.ix.52	Blue or fin?	1	8-9	S	—
1.x.52	Fin	1	3	S	Length approx. 70 ft.
3.x.52	Fin	2	10	S	Cow and calf
4.x.52	Fin	1	20	S	—
5.x.52	Fin	2	—	S	—
	Fin	2	—	S	—
	Fin	1	—	S	—
	Fin	1	—	S	—
	Fin	1	—	S	—
	Blue	2	—	S	—
6.x.52	Fin	2	10-11	S	—
10.x.52	Fin	2	6	S	Cow and calf

season. In neither case were the killer whales seen to be successful in their attacks.

(*b*) *Fin Whales* (Balaenoptera physalus *Linné*) *and Blue Whales* (Balaenoptera musculus *Linné*)

These were sighted only in September and October and were all travelling south. Table 6 gives details of those sighted.

(*c*) *Minke Whales* (Balaenoptera acutorostrata *Lacépède*)

On August 25, 1952, three minke whales were closely observed by the author from the aircraft. These whales, approx. 25-30 ft in length, had the characteristic white band across the flippers. They were in shallow water very close to the reef and were moving south. Another minke whale was sighted off Point Cloates on August 30.

IV. ACKNOWLEDGMENTS

The author wishes to express his gratitude to Mr. J. F. Pekin, pilot of the spotting aircraft, for his enthusiastic cooperation in the collection of these records, and also to the Norwest Whaling Company for their cooperation and for the use of facilities at their station.

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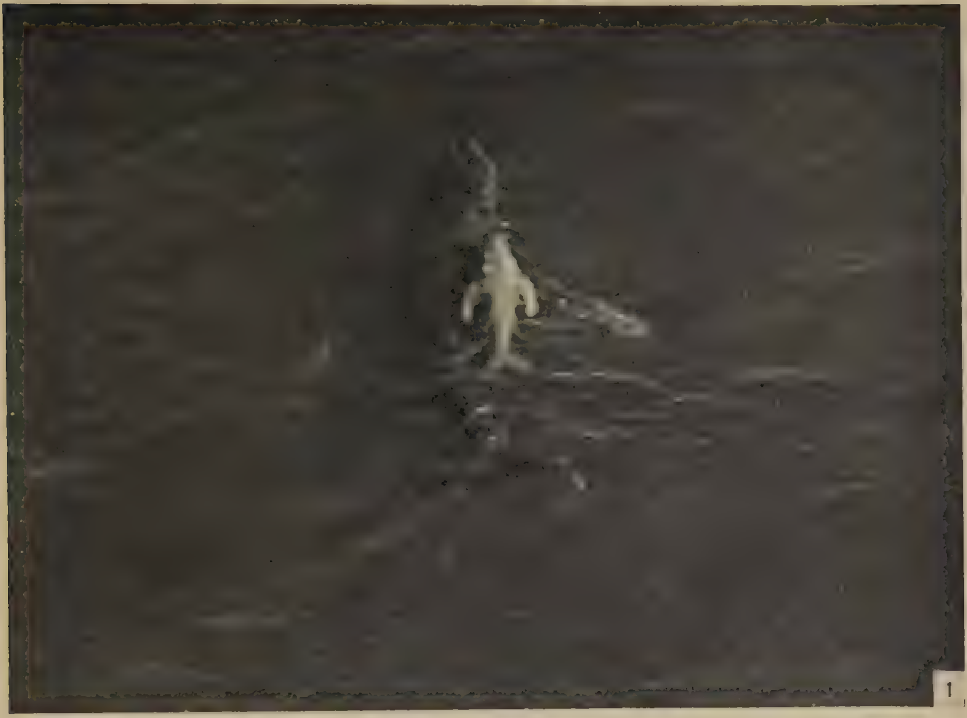
AERIAL OBSERVATIONS ON THE HUMPBACK WHALE



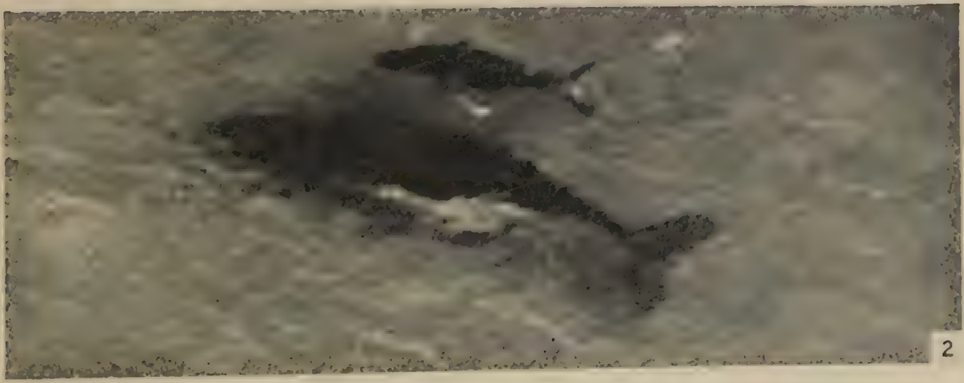
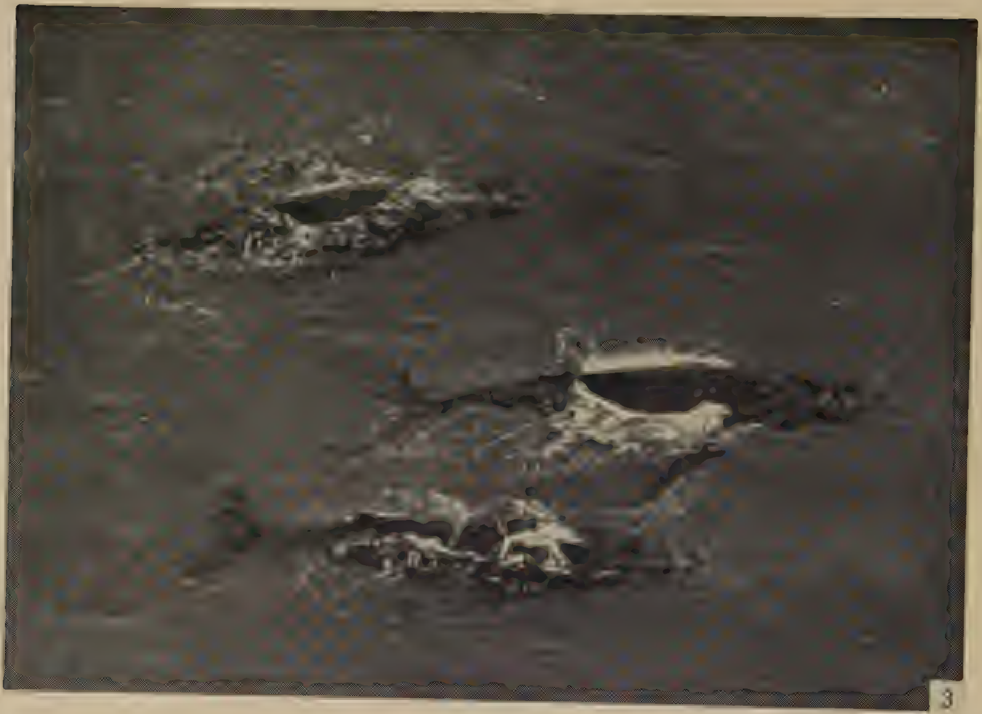


Fig. 1.—Aerial photograph of female humpback whale with very young calf, Western Australian coast. (Photos: S. Fowler.)

Fig. 2.—Aerial photograph of humpback whale and calf; Shark Bay, Western Australia.

AERIAL OBSERVATIONS ON THE HUMPBACK WHALE



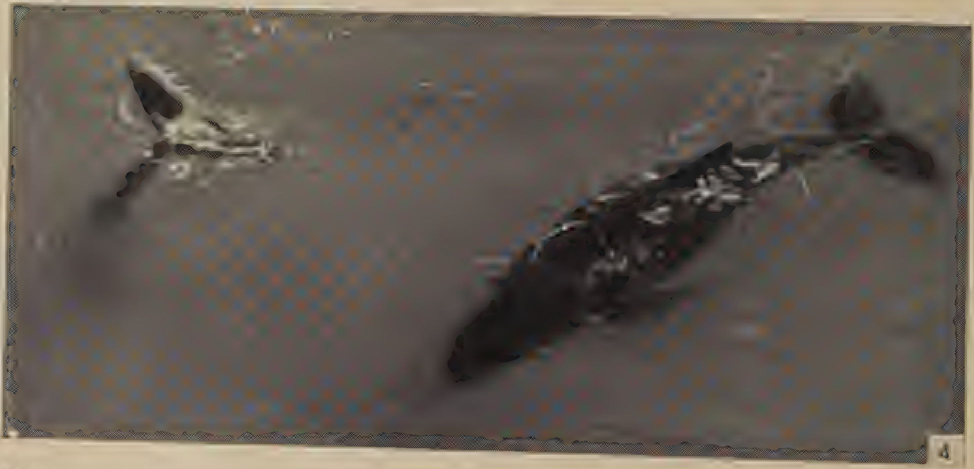


Fig. 3.—Aerial photograph of three humpback whales at the surface, Western Australian coast. (Photos: S. Fowler.)

Fig. 4.—Aerial photograph of two humpback whales sounding, Western Australian coast.

THE OYSTER BLENNY, *OMOBRANCHUS ANOLIUS* (VALENCIENNES) (BLENNIIDAE)

By J. M. Thomson and A. E. Bennett*

(*Manuscript received February* 9, 1953)

Summary

The oyster blenny, *Omobranchus anolius* (Valenciennes), commonly uses the shells of the oyster *Crassostrea commercialis* (Ireland and Roughley) as a nesting place. The male parent guards the eggs during development. The eggs are laid in batches which hatch over a prolonged period. A daily rhythm in hatching is apparent, with most eggs hatching in the early evening. Some aspects of the development of the eggs and larvae are reported upon, particularly the formation and fate of the pigment patches. On hatching, each larva is taken into the mouth of the parent and expelled from the nest, apparently to remove from the larva an amorphous material which clings to it. Larvae were kept alive in the laboratory successfully for only 3 days after hatching.

I. Introduction

The oyster blenny, *Omobranchus anolius* (Valenciennes), which is common in bays and estuaries in southern Queensland and New South Wales, inhabits the tidal mud-flats, particularly where shellfish beds occur. The common name derives from the use of empty oyster shells as hiding places and nests. It can survive during low tide in the small amount of water in an oyster shell or in a shallow pool scarcely deep enough to cover the fish. This faculty is possessed by other blennies, for instance, *Epigeichthys atropurpureus* (Kittlitz) from western North American coasts (Ricketts and Calvin 1948), and *Petroscirtes mitratus* Rüppel in South Africa (Smith 1950).

The course of development and hatching in three wet nests discovered in October 1951 was followed in as great detail as the demands of other work permitted. The first nest was found about a week before the other two, and only one of the three still had the guardian parent in attendance when transferred to the laboratory.

II. The Eggs

The eggs were laid on both the upper and lower valves of the shell, in a single layer. Of the two nests found later, that which was unattended had 135 eggs on the lower valve and 65 on the upper; while from the nest with the attendant parent 468 larvae hatched and a number of undeveloped eggs and empty cases were deposited about half way through the hatching period. Gudger (1927) reported that 686 eggs were laid in an oval mass by a female *Pholis gunnellus* (Linnaeus) and another blenny, *Anoplarchus purpurescens* Gill, was found to lay from 800 to 3000 eggs.

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The eggs of the oyster blenny are deposited in patches set close together without recognizable patterns either in the relation of the patches to each other or in the relative positions of the eggs within the patches. Viewed from above, the outline of each egg is circular (0.8 mm dia.) along the free edges but flattened where adjacent eggs touch (Fig. 1*A-D*). Viewed laterally (Fig. 1*E*) the eggs show a flattened base, sides with slight curves, and a broadly domed top (ht. 0.5 mm). The upper two-thirds of each egg is quite clear, but the interior is obscured on the lower third by an opaque creamy-white substance closely adherent to the egg-case, which glues the eggs both to the substrate and to each other.

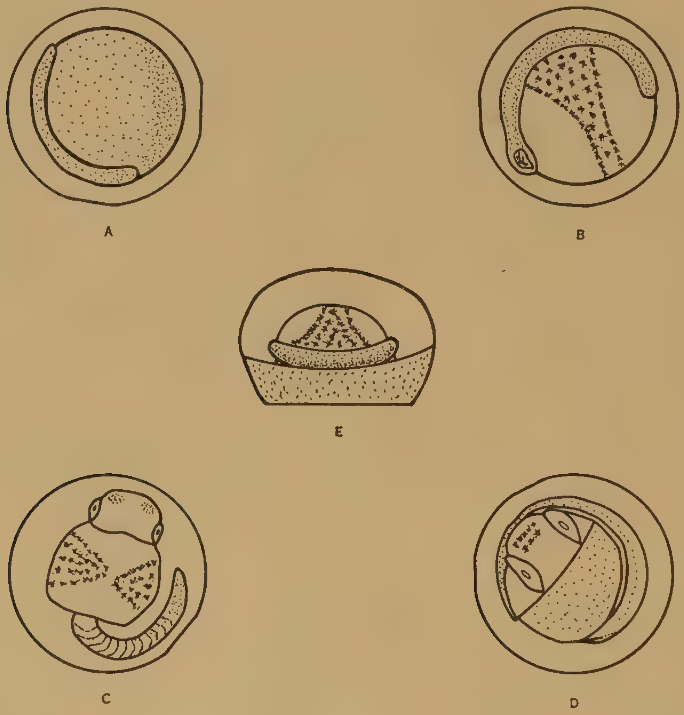

Fig. 1.—Eggs of *Petroscirtes anolius*: *A*, stage before melanophores appear; *B*, early eyed stage showing band of melanophores; *C*, later eyed stage showing melanophore band parting ventrally on yolk; *D*, ready to hatch, the tail long and curved past head, yolk as a pouch ventrally at posterior end of head; *E*, lateral view of egg at stage (*b*).

When deposited the eggs are rich yellow, deepening to bright orange after division commences. As growth of the embryo proceeds, the yolk becomes covered in a melanic pigment pattern which becomes intense by the time the eyes have developed. In appearance the egg capsules are tough and smooth, without obvious structure; the adhesive material is finely granular and there are no oil globules in the yolk.

III. DEVELOPMENT OF THE EGGS

The lightly melanized stage of the egg's development occurs when the embryo has extended about two-thirds of the way around the yolk-sac. It takes the form of a narrow band extending around the yolk at right angles to the long axis of the developing embryo.

The heavily melanized stage follows within a few hours. The pigment band is much more dense and is wider. This stage merges into the next when the eye is discernible as an established structure. The melanized band now breaks into two (Fig. 1*C*), a gap forming on the side of the yolk-sac remote from the embryo.

As development proceeds this gap widens as the melanophores migrate towards the embryo. In the dark-eyed stage the eyes have become heavily pigmented; the tail of the embryo lies freely and is curved so as to pass right around the mouth (Fig. 1*D*). At this stage the yolk-sac is much reduced, being in the form of a wide pouch ventrally. Segmentation is apparent in the tail region and some very slight pigment is evident as a row of spots ventrally along the tail. The melanophore band across the yolk has entirely disappeared, and seems to be directly utilized as the chromatophores of the pectoral fins and the gut cavity lining immediately underlying the fins.

TABLE 1

NUMBER OF EGGS IN ONE NEST

	Clear Yolk	Lightly Melanized	Heavily Melanized	Eyes Formed	Eyes Dark
Upper shell	40	13	19	38	18
Lower shell	15	14	3	23	10

It was judged unwise to disturb the brooding parent in order to count the eggs in each stage, but in the unattended nest the numbers in Table 1 were counted in various arbitrarily distinguished stages.

The nests of eggs were collected on the afternoon of October 8, 1951. Hatching commenced within a few hours in the attended eggs. None of the unattended eggs hatched until late the next day. Hatching of the unattended eggs continued for 4 days (a large proportion of the eggs from this nest had hatched before collection). The attended eggs continued hatching over a period of 17 days from October 8 until October 25.

Hatching was not evenly distributed throughout the day. It will be seen from Figure 2 that on each day between October 8 and 16 the hatching occurred at its greatest rate between 5 p.m. and 9 p.m., with the peak between 5.30 p.m. and 7.30 p.m. Table 2 shows the number of fish hatched per 24-hr period ending 9.30 a.m.

IV. Parental Care during Hatching

The use of shells as "nests" for depositing eggs is well known for several species of blennies. Sometimes the males, sometimes the females, and sometimes both sexes guard the eggs of the blennies (Guitel 1892, 1893; Gudger 1927; Brown 1929; Schultz and DeLacy 1932).

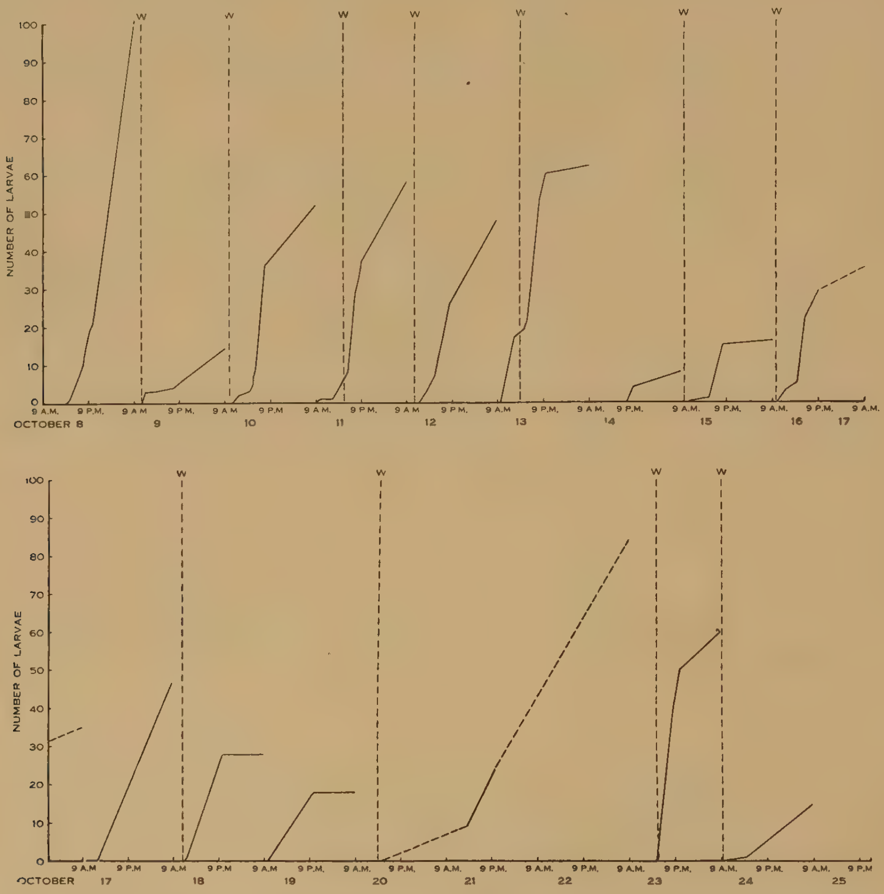

Fig. 2.—Cumulative hatching rate for 24-hr periods ending 9 a.m., October 8-25.

In this species the role of the parent was found to be more than the simple one of guarding the eggs. He was observed for lengthy periods to be creating a current of water over the eggs by gentle movements of the tail. The existence of the current was clearly revealed by the behaviour of small particles in the water adjacent to the nest.

Presumably the parent also serves to repel intruders in the natural habitat. He was frequently to be seen peering from the shell at the surroundings, but was seldom seen away from the shell for more than a moment or two.

Each larva, as it is hatched, is taken into the mouth of the parent and then expelled from the nest with a sharp spitting movement. This was seen many times by both authors and checked with a series of "births" during the peak hatching periods. It is concluded that each larva undergoes this treatment.

TABLE 2

HATCHING OVER 24 HR

October 9	101	October 18	47
10	4	19	48
11	52	20	0
12	58	21	?*
13	48	22	15
14	60	23	69
15	10	24	14
16	26	25	1
17	35	26	0

* Some of the fish attributed to October 22 could have been produced on the previous day.

The function of this behaviour would have remained obscure were it not for the fate of the unattended eggs in the other two nests collected. These eggs hatched, but the larvae moved feebly and within an hour or two were dead. These proved to be covered in an irregular layer of structureless material presumably derived from the yolk. This substance enveloped all the young from the unattended eggs and none of those which had passed through the mouth of the parent, so it is presumed that the function of the parental licking is to remove this flocculent material. The parent did not seem to guard, otherwise assist, or attack the larvae which were swimming about the dish. Nor did other adult blennies attack any of the larvae introduced into a dish with them.

V. LARVAL DEVELOPMENT

The larvae were variously treated after hatching. All except the last few were removed from the dish containing the nest at the time of changing the water. Some were placed in shallow dishes, some in watch-glasses, and some in erlenmeyer flasks. They were offered as food various cultures of ciliates and flagellates, small pieces of algae with the attached epiphytes, or fresh microplankton. No larva developed beyond 3 days. Probably this marked the length of time which they could be supported by the yolk remaining in the yolk-sac after hatching.

(*a*) *At Hatching*

Several larvae were measured immediately after hatching and all were found to be 3.2 mm long. The yolk-sac was still very distinct at this stage (Fig. 3) and was expanded laterally beyond the side margins of the head. There was a small scattered patch of melanophores dorsally on the frontal region of the head; the prominent eyes were very black, with iridescent specks of gold and blue. Otherwise the head was unmarked. The internal organs had a yellow coloration (xanthin?). The yolk-sac was orange in colour while the larva was alive, but faded to a pale yellow on preservation in formalin. The pectoral fin was outlined with dense black melanin and internally adjacent to these fins was a pigmented area, probably the lining of the gut cavity. This internal pigment and the yellow colour of the internal organs were visible only in live specimens; the opacity of the flesh after death and preservation concealed their presence. There appeared to be 32 myomeres behind the head region, but the rearmost were very difficult to distinguish. The dorsal and ventral fin folds were large compared with the depth of the body and were continuous with the tail fin.

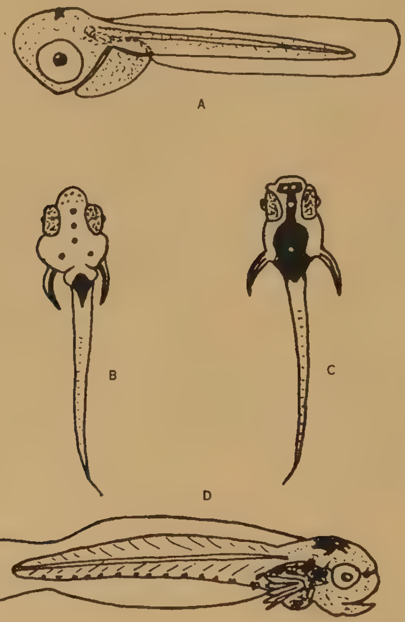

Fig. 3.—Early larvae of *Petroscirtes anolius*: *A*, newly hatched larvae; *B*, 4 hr after hatching; *C*, 5 hr after hatching; *D*, 3-day larva.

(*b*) *Four Hours after Hatching*

The yolk-sac had diminished greatly. The golden iridescent flecks in the eye were more concentrated in the lower half. The melanophores at the anterior end of the head were more distinct. Viewed from below, a row of three median melanophores could be seen on the head, with posteriorly a somewhat larger pair. The pectoral fins had lengthened and the melanophores were spreading further over them. The adjacent internal pigmentation had become more dense. The 26 rearmost myomeres of the tail had distinct melanic spots at the ventral edge of each myocomma

(Fig. 3). In the course of 5 min the paired chromatophores under the head spread and met. However, it was observed in specimens kept under continual observation that the size of this pigmented area shrank while active swimming took place, though in the course of 1½ min after settling down again the chromatophores expanded to meet once more.

(*c*) *Five Hours after Hatching*

The only obvious difference from the 4-hr larva was the greatly increased area covered by pigment. The anterior melanophores had fused to form a plate with two small unpigmented patches (Fig. 3*C*). This connected with a vase-shaped pigmented area embracing the region where the isolated median and paired melanophores appeared in the 4-hr larva. The internal pigment in the trunk region was now very dense.

From this stage there was little change in external appearance until death occurred 2 days later. There was slight growth, the larvae at death being 3.5-3.7 mm in length. The yolk had been completely absorbed by the second day. The melanophores along the tail became more distinct. Internally the intestinal loop became visible. The continuous fin fold showed dorsal and ventral constrictions where the adult tail fin would terminate.

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PILCHARD SHOALS IN SOUTH-WEST AUSTRALIA

By A. M. RAPSON*

(*Manuscript received January* 19, 1953)

Summary

The distribution of pilchard shoals from echo-sounder records, obtained on the Fisheries Research Vessel *Warreen* between Albany and Esperance, is described. Data from echograms and ring net catches are used to estimate the density of fish in shoals. A method of estimating the number of shoals of pilchards per acre has been developed, using the sounder as a surveying instrument, and the quantity of shoal pilchards on two parts of the coast has been calculated. Dispersal of shoals when feeding conditions are good is deduced after examination of pilchard stomachs and N70 tow net hauls. Movements along the coast are inferred from the distance shoals must travel to obtain a full feed. The selection and avoidance of certain classes of food are discussed. The manner in which shoals come to the surface is described, and observations are made on behaviour of fish in surface shoals.

I. INTRODUCTION

Fisheries Research Vessel *Warreen,* during part of cruise 38, carried out semicommercial trials with a Scottish ring net in connection with echo-sounding. No great success was achieved although the method shows considerable promise in south-west Australia. Using the echo-sounder as a biological tool, however, some of the relationships between tuna and pilchards are explained, and an estimate is made of the quantity of pilchards present; set nets were used to determine the density of distribution where shoals were scarce and, from the average size of shoals and quantity of fish they contain, an attempt is made in Section VIII to calculate the number of pilchard shoals per acre.

Pilchards (*Sardinops neopilchardus* Steindachner) gave a sharp, black echogram and with the exception of blue sprat (*Stolephorus robustus* (Ogilby)), which gave a somewhat fuzzy trace, no other species was recorded. Salmon (*Arripis truttæ* Bloch & Schneider), ruff or night herring (*Arripis georgianus* Valenciennes), and several kinds of leather-jackets constitute the principal commercial species in these waters, but no echograms of them were recognized. *Warreen* was in south-west Australia from March 1 until June 27, 1951, but most of the data used in this work were collected from May 10 to June 20.

II. MECHANICS OF THE SOUNDER

Although the air bladder is believed to be the principal organ reflecting the sound beam (Tucker 1951; Marshall 1951) it is not impossible that, in their respiration, fish shoals produce a great quantity of small gas bubbles which could give an echo (see Raitt 1948, p. 407; Dietz 1948, p. 441).

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However, no modification of ping or bias by which different types of organism may be detected was attempted and this may be one reason why larger species of fish were not recorded.

Some characteristics of the equipment used are described and some echograms interpreted as follows. The sound beam leaves the transmitter at an agle of 40°, forming a cone, but after several fathoms the beam is confined mainly to a cylinder about 13 ft wide which continues almost to the limit of the effective range.

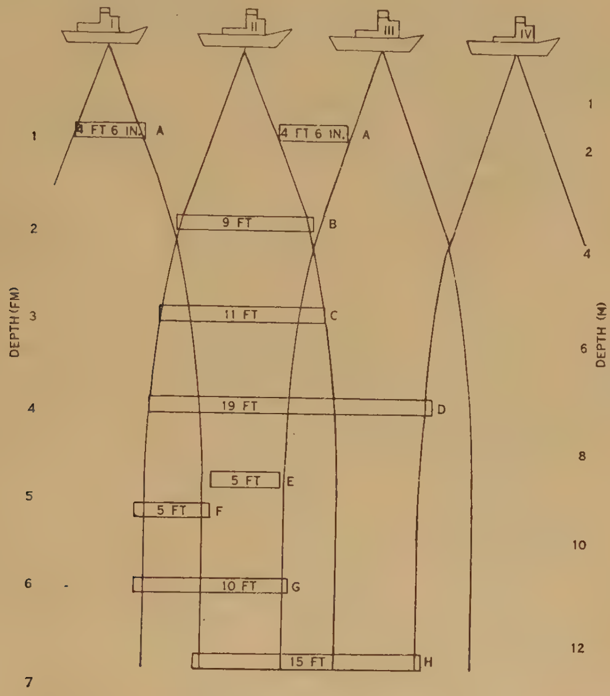
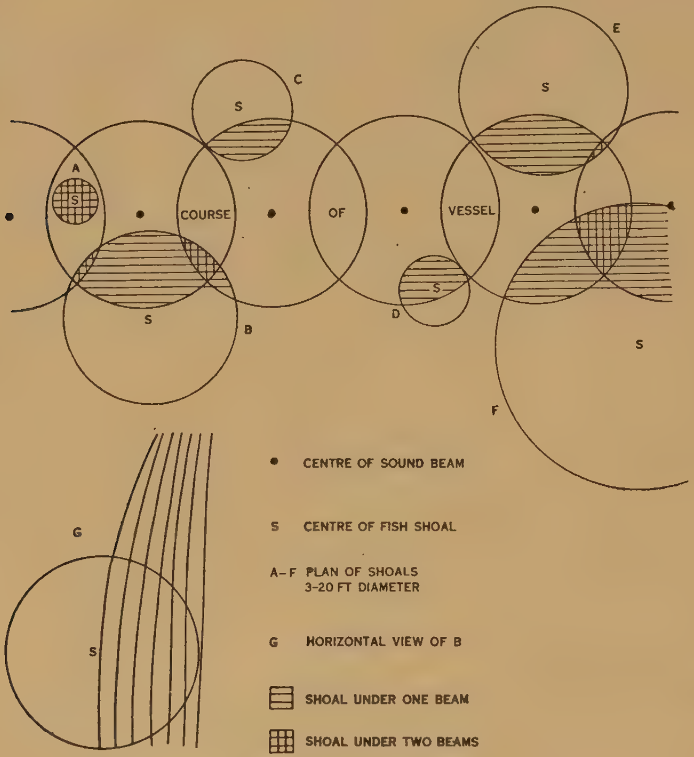


Fig. 1.—Elevation of four successive sound beams and the covering effect at 6 kt on shoals at different depths.

Figure 1 represents in profile four successive beams which show the coverage at different depths, and Figure 2 shows a plan of shoals of different sizes in the track of a vessel and the area covered by the sound beam below 5 fm.

Few shoals were recorded by the machine in less than 5 fm although at times the vessel steamed through surface and near-surface shoals, which suggests that at shallow depths, perhaps because of the thin density of fish, a large proportion of the sound beam must be covered and also the shoal must extend over a considerable area in excess of the beam to give sufficient resonance to produce an echo.

The vertical diameter of the shoal recorded is a more accurate visual guide to the size than the number or density of stylus marks, and probably represents an average of 80 per cent. of the actual vertical diameter (Fig. 2*G*) (but see Tester 1943). Aerial, sea, and sounder observations suggest that the shoals are spheroidal, the vertical diameter being sometimes more and sometimes less than the horizontal.


E
S
C
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A
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COURSE
OF
VESSEL
S
S
B
D
S
S
F
G
S
● CENTRE OF SOUND BEAM
S CENTRE OF FISH SHOAL
A–F PLAN OF SHOALS 3–20 FT DIAMETER
G HORIZONTAL VIEW OF B
SHOAL UNDER ONE BEAM
SHOAL UNDER TWO BEAMS

Fig. 2.—Diagram of fish shoals under sound beams.

In estimating the abundance* of shoal fish from the sounder the following errors must be considered:

* The quantity of pilchards in a shoal has been calculated on the following basis. The average number of stylus marks in some large shoals in the Albany area was 2.7, which at 9 ft between marks makes the observed average horizontal diameter of 24.3 ft. If the diameter measured is 80 per cent., this gives a probable value of 30.4 ft. At 30.4 ft diameter the error due to overlap is about 5 per cent., making an actual value of 29 ft horizontal diameter. The average vertical diameter recorded by the sounder was 32 ft.

Near Esperance 10 shoals had an average of 1.5 stylus marks per shoal; calculating as before, with a 25 per cent. error due to overlap, gives a horizontal diameter of 11 ft. The average vertical diameter recorded by the sounder was 10 ft.

It has been assumed that shoals with a diameter of 36 ft will be recorded in a zone approximately 60 ft wide or 30 ft on either side, measured from the centre of the vessel, and 20 ft diameter shoals about 14 ft on either side of the centre of the vessel (but see Cushing 1952).

(*a*) The stylus indicates larger shoals than are present because of the overlap between successive sound impulses (up to 25 per cent. at 6 kt).

(*b*) The horizontal and vertical diameters of each shoal recorded will be on an average about 80 per cent. of the actual diameter.

(*c*) Although the sound beam covers a strip 13 ft wide at 5 fm, shoals partly outside this area will be recorded.

The echo-sounder does not detect dispersed fish and the evidence suggests that the relatively small shoals in the Esperance area are near the limit in density and size at which fish may be detected satisfactorily. Few intensely dark shoals were recorded, but many shoals were present and the actual quantity of fish may have been greater than in a comparable area near Albany.

III. ECHOGRAMS

Figure 3 gives a pictorial representation of the number of shoals recorded, using Krefft and Schuler's (1951*a*, 1951*b*) method. In south-west Australia pilchard shoals were rare in water over 35 fm deep and at more than 5 miles from land. They were most plentiful in bays, but dispersed fish with only a few shoals occurred over a wide area between Albany and Doubtful I. The surface shoals off Starvation Boat Harbour, and the great area of surfaced fish observed from Cape Arid to Culver Point in 1945, indicate that quantities of pilchards occur on this coast.

TABLE 1

AVERAGE DEPTH OF PILCHARD SHOALS IN SOUTH-WEST AUSTRALIA

Locality	Number Measured	Vertical Diameter (ft)
Albany	77	19.5
Two People Bay	8	17
Cape Riche	3	30
Dillon Bay	16	17
Bremer Bay	15	26
Doubtful Bay	10	10
Esperance Bay	32	12
Ram I.	1	18

Appendix I gives the details from which Figure 3 was prepared. No extensive fishing was carried out, but the size of shoals for the principal areas is given in Table 1. Three large shoals were recorded at Cape Riche, and in sheltered waters the largest shoals occurred in Bremer Bay. The greatest number of records were obtained near the entrance to King George Sound and in Esperance Bay, where the average shoal diameters were 19.5 and 10 ft respectively.

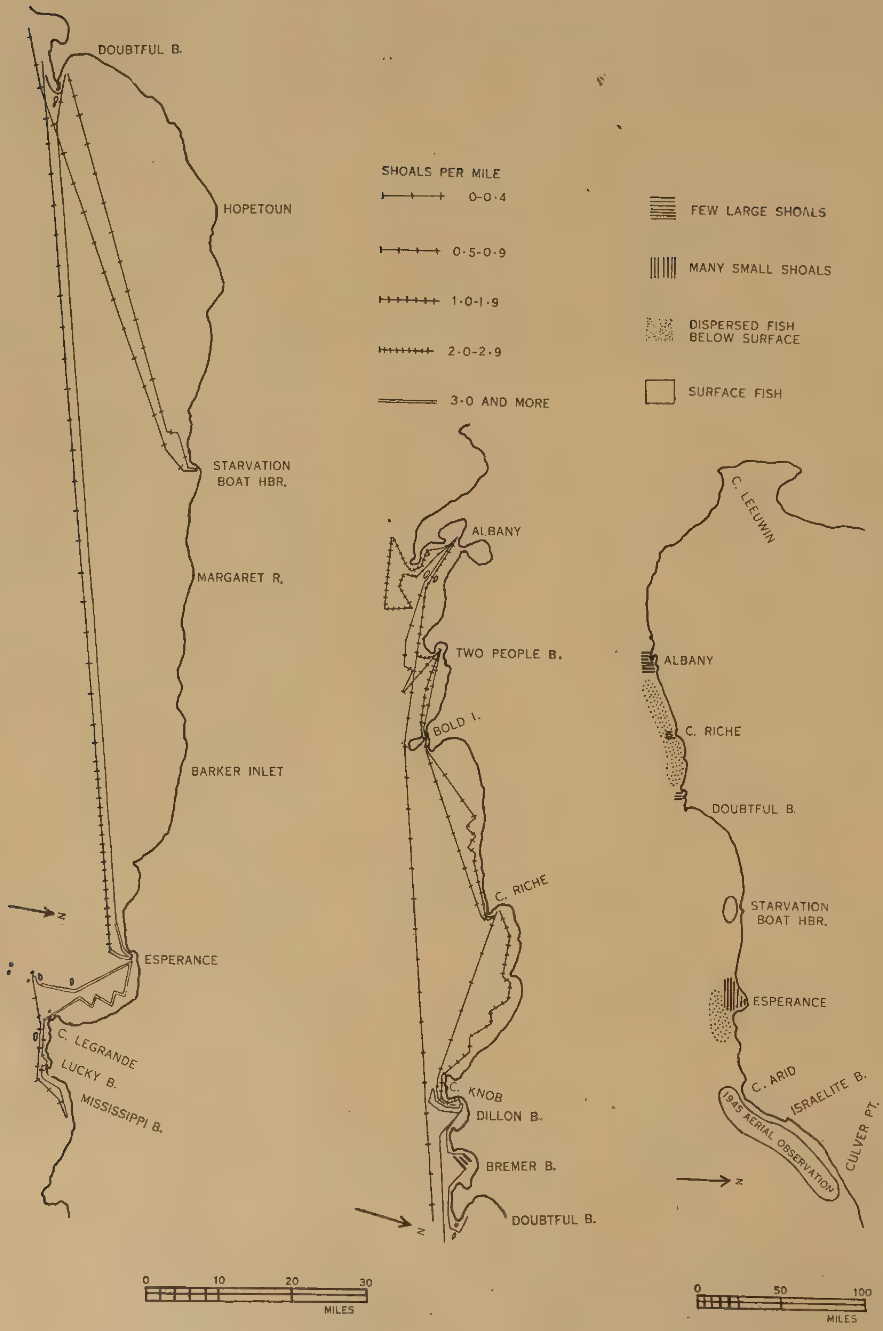
DOUBTFUL B.
HOPETOUN
STARVATION BOAT HBR.
MARGARET R.
BARKER INLET
N
ESPERANCE
C. LEGRANDE
LUCKY B.
MISSISSIPPI B.
SHOALS PER MILE
0-0·4
0·5-0·9
1·0-1·9
2·0-2·9
3·0 AND MORE
FEW LARGE SHOALS
MANY SMALL SHOALS
DISPERSED FISH BELOW SURFACE
SURFACE FISH
ALBANY
TWO PEOPLE B.
BOLD I.
C. RICHE
C. KNOB
DILLON B.
BREMER B.
DOUBTFUL B.
N
0
10
20
30
MILES
C. LEEUWIN
ALBANY
C. RICHE
DOUBTFUL B.
STARVATION BOAT HBR.
ESPERANCE
C. ARID
ISRAELITE B.
CULVER PT.
1945 AERIAL OBSERVATION
N
0
50
100
MILES

Fig. 3.—Pilchard shoals, Albany to Esperance, May and June 1951.

The large area with dispersed fish between Albany and Doubtful I. was traversed on four occasions in March and May and on these passages pilchards were widely distributed and were being preyed on by tuna and birds; relatively few echograms were obtained. For this reason the echograms give only an imperfect picture of the quantity of fish present, but they do indicate clearly the possibilities for ring netting. Plate 1, Figure 1, is an echogram of eight shoals of pilchards in Esperance Bay.

Manteufel (1941, Fig. 20) gives a diagram of echo soundings showing shoals of herring 3-35 m long and 2-7 m deep, only a few metres separating the different shoals. They would be recorded in positions as *A*, *C*, and *E* in Figure 2. No comparable echogram was obtained in south-west Australia. The most numerous shoals in Esperance Bay are shown in Plate 1, Figure 1; the closest are about 70 ft apart. In shooting a ring net there would be little chance of taking two shoals unless they merged after the record was taken. For comparison, Plate 1, Figure 2, is a record of a series of pilchard shoals from Hodgson (1950, p. 12). In both cases the water is 15-17 fm deep.

IV. RING NET RESULTS

The Scottish ring net could be shot and pursed in 20 min and the catch brought alongside in about 30 min, compared with nearly 3 hr for the large purse-seine net such as was used by the commercial vessel *Jon Jim*. It was necessary to shoot in water deeper than 13 fm as the net tore easily if it touched the bottom and, over 18 fm, fish escaped under the lead line. In deep water meatmeal was used to attract fish to the surface; it may have been successful, but none was eaten. Fluorescein also was used to mark the position of a shoal detected on the sounder but it is probably not necessary for an experienced observer.

In shooting a net over a shoal located by echo-sounder, Hodgson (1950) says it is advisable to make two runs over the shoals before shooting the net; the second sometimes dispersed the shoal, and the third almost invariably did. Results in south-west Australia indicated that the shoals are usually easily frightened and, except for times when the pilchards "swim", to shoot immediately the vessel is turned after locating a shoal, when conditions of wind and tide are favourable, is productive. In fact to shoot on the first indication would be desirable if it were practicable.

Table 2 gives details of hauls with the ring net. During the whole investigation, 15 hauls produced nearly 17 tons and 30 hauls were unproductive. The *Jon Jim*, with the purse seine 22 fm deep, confined operations to King George Sound and caught 50 tons from hauls on 29 days. Neither net caught more than 6 tons at one shot; comparable catches have been made on other parts of the coast. By using lights, ring net hauls of 6 and 9 tons of pilchards have been made in Port Phillip, but several of 12 tons, mainly pilchards, were made in the Gippsland Lakes. Table 3 gives a summary of the quantities taken by *Warreen*, and Plate 2, Figure 1, shows pilchards being brailed from the net on to the deck of *Warreen* in King George Sound. In the New Zealand Marlborough Sound, where a pilchard industry flourished for several short periods, hauls of over 10 tons were exceptional and the usual maximum size was about 5 tons. Small nets which could be shot quickly had some advantage over the big nets 20-25 fm deep.

TABLE 2

RING NET RESULTS: MAY-JUNE 1951

Date	Locality and Depth	Catch	Remarks
10.v.51	King George Sound 18 fm	11 Frigate mackerel	Pilchards and true mackerel seen near surface although net shot originally on sounder trace. Fish meal and solid fluorescein, which sinks too quickly, put in water
17.v.51	King George Sound	8 Boxes pilchards	Pilchards not on surface and net was shot on sounder trace, but fish moving about in large quantities in region
17.v.51	King George Sound 16 fm	5 Tons pilchards	Shot on surface shoal. Fish appeared to move in and out of net apparently at will until pursing almost complete, at which stage white paddle kept them in net
20.v.51	Dillon Bay 20 fm	No catch	Fish showed on sounder, fluorescein marked spot encircled, fish escaped. Bright sunshine, wind and sun together, so shot possibly not favourable for catching pilchards
25.v.51	East of Doubtful Bay 30 fm	No catch	Net shot on sounder trace. Wind 3-4, heavy southerly swell, nearly lost net. Too deep
4.vi.51	Two People Bay 20 fm	No catch	Some shoals showing on surface, but net shot on a small sounder trace, better surface shoals then showed behind vessel
5.vi.51	Off Cheyne Beach 20 fm	No catch	Net shot Cheyne Beach, Bold I., large number of shoals about, clear water, fish moving fast
8.vi.51	Dillon Bay 14 fm	No catch	Shot on fluorescein
15.vi.51	Esperance Bay 14 fm	200 Lb	Shot on fluorescein with meal
17.vi.51	Bremer Bay 14 fm	1100 Lb	Shot on fluorescein, fish came to surface during shot

V. DENSITY IN SHOALS

The largest shoals recorded by the sounder, 36-42 ft in diameter, probably contain about 5 tons of pilchards, which represents about 1 lb, or 12 average-size pilchards, in 2.2 cu. ft of water (calculated for a diameter of 36 ft). Runnstrom (1941) says 2 herrings per cu. m (1 in 18 cu. ft) occur in good shoals off Norway, and Balls (1948) suggests that

4 herrings per cu. ft may sometimes be present. The density of pilchards present in south-west Australian shoals may be slightly more than this in number, but in weight 1 cu. m would contain about 16 lb of pilchards. For comparison, the only other species which has been caught in quantity with a ring-type net in Australia is the horse mackerel (*Trachurus novaezelandiae* Hutton); a net 23 fm deep and 240 fm long has taken quantities up to 30 tons, which indicates a minimum of one fish of 1½ lb per cu. m. These calculations indicate that even in good shoals of fish 0.1 per cent. in Runnstrom's example, and 0.73 per cent. of the volume occupied by pilchard shoals in south-west Australia, is actually occupied by fish. von Brandt and Scharfe (1951) showed that with traps less than 2½ m apart at 23 fm the fish in them showed as a shoal, but that a vertical arrangement could increase the apparent density. The size of fish is not clearly stated, but in Western Australia, as far as could be judged, no results showing such wide dispersal were obtained.

TABLE 3

SUMMARY OF HAULS WITH SCOTTISH RING NET WHEN FISH WERE CAUGHT, MARCH-JUNE 1951

No. of Hauls	Approximate Weight	Total Weight		
		Tons	Cwt	Lb
2	Less than 1 cwt	—	—	85
5	1-6 Cwt	—	14	—
3	½ Ton	1	10	—
3	1-1½ Tons	3	9	—
2	About 5 tons	11	—	—
15 Hauls for		16	13	85

Drift nets, used as set nets, provide further data on the density in which pilchards occur (Table 4). In the vicinity of shoals of fish recorded by the sounder, 4 nets produced approximately 80 lb of fish; where no shoals were recorded by the sounder the catch was 8 lb. On occasions the drift nets may have been set near a shoal which was missed by the sounder, but the difference in catch probably indicates a dispersal not sufficiently dense to be recorded by the echo-sounder. On the basis of the ring net catches the sounder may be said to record shoals where the density is five fish per cu. ft of water, but with the set nets no indication is obtained when the quantity is 1/20 of this or one fish in 4 cu. ft. One fish in 4 cu. ft is a density of 0.07 per cent. fish, so Runnstrom's 0.1 per cent. may be near the limit of echo sounding except for very big shoals. Plate 2, Figure 2, shows the drift nets hauled on board and the few fish they contain, while for comparison Plate 3 is part of a ring net with nearly half a ton of small pilchards meshed while fishing in Queen Charlotte Sound, New Zealand, when the net was nearly lost. The *Jon Jim,* fishing in King George Sound, also obtained small quantities of meshed fish on several occasions. The small size of Esperance shoals may be due to bottom configuration, as the waters in the Bay and throughout the Recherche Archipelago are relatively shallow compared to the deeper inshore waters between Albany and Doubtful I.; but the cause of the small shoals may be related to food supplies or to seasonal variation in habits. There is, however, a possibility of racial difference (see Balls 1948).

TABLE 4

SET NET RESULTS: MAY-JUNE 1951

Date	Locality	Pilchard Catch	Remarks
14.v.51	Limestone Head, King George Sound	68 Lb	Four nets set previous evening close inshore, originally to determine if fish were on the bottom when no traces were found on the sounder, but shoals appeared on sounder in vicinity before nets hauled
4.vi.51	Two People Bay	74 Lb	Four nets set on trace from sounder in about 12 fathoms near head of bay. Fish later came to surface in quite dense shoal but submerged before ring net could be set
5.vi.51	East of Cape Riche	Nets lost	Fresh easterly in morning; no trace of nets
13.vi.51	Lucky Bay, east of Esperance	64 Pilchards	Three nets set; no traces of pilchards in bay but sounder records outside
14.vi.51	Sandy Hook I., (off Esperance Bay	20 Pilchards	Three nets; no trace of pilchards on sounder within several miles before setting and hauling

Few shoals were recorded after heavy seas and the pilchard may then rest near the bottom, but in shallow water this is unlikely and the shoals probably remain dispersed, when they would not be detected.

It is of interest that in highly productive fish ponds 4000 lb fish per acre are produced per annum (Hickling 1948), and if all fish are present at one time in ponds 6 ft deep this is equivalent to 0.25 per cent. of the water being occupied by fish.*

VI. SURFACE SHOALS

Blackburn and Rayner (1951) say "the surface display is misleading, giving the appearance of more fish than are actually present." Most spectacular surface shoals were seen in King George Sound on May 11; the *Warreen* and *Jon Jim*, ¼ mile apart, caught almost simultaneously about 5 tons of pilchards each, and during the hauling of the nets the surface over an area of about 800 by 100 yd showed many shoals of fish. These shoals were described by various observers as consisting of hundreds to many acres of fish. The actual surface at no time was more than one-quarter covered with fish so that the area of fish was about 4 ac. Probably not more than 10 shoals, containing about 50 tons of fish, were present in this display, and the surfacing may have actually comprised the greater part of the fish in the Sound. The echo-sounder was not of much use in this instance, for, after shooting the net on an echo trace, the fish came near the surface before the first shot was complete, when eight boxes were obtained, and in the second shot it was difficult to select where the fish were most dense.

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* Calculations have been made on the basis of equal weight of fish per equal volume of water.

Some idea of the surface area which may be covered by a compact spherical shoal 20 ft in diameter containing 75,000 pilchards may be gauged by allowing each pilchard 6 by 1 in. of surface; the original spherical shoal, represented in plan by a circle of 20 ft diameter, would cover an area of over 3000 sq. ft. If only one-quarter of the surface is covered the area becomes 12,000 sq. ft and may be represented by a circle about 125 ft in diameter or rather more than $\frac{1}{4}$ ac. Aerial observations of a spherical shoal surfacing has been described by Mr. R. Hunt of Albany (personal communication) as "erupting from a cone and spreading out in waves until none of the original shoal remained; the area covered is large, but difficult to keep in view as the position and shape change."

In the surface shoals fish may swim in compact formation of six to eight or more side by side, and quite extensive areas of surface are covered by fish swimming side by side and head to tail. At least part of the noise of such a surface shoal is made by the gulping of air and water. Evening shoals of pilchards were observed near Albany jetty acting in a similar manner, and many were scooped with a dip net. The fish seemed to be in a semicomatose state and frequently returned near to the vessel; gulping of air and water occurred as in the open Sound, and the fish remained on the surface for nearly an hour. No satisfactory explanation of the "swim" has been found, unless it is that the shoal formation is too compact and the fish sometimes need to swim freely. Tow net samples taken at a depth of 12 fm after the "swim" on May 11 contained many faeces, which had not been taken previously, although detritus consisting of broken diatom cases and crustacean remains were not uncommon in the Sound. In this case the "swim" may have been a necessity associated with defecation in a compact shoal. Other shoals were observed at the surface in the vicinity of Doubtful I. The sea was calm and the water clear, but the fish were moving in an extremely irregular manner and at some speed. They may have been feeding or chased by larger fish, but none was captured. Shoals extending over 2 miles by $\frac{1}{2}$ mile of surface were observed off Starvation Boat Harbour in May 1951. No record showed on the echo-sounder, although the fish submerged on the approach of the vessel. These shoals, which numbered between 60 and 80, were more widely scattered and contained a much smaller quantity of fish than in King George Sound, but were behaving in a similar manner.

Observations on pilchards in south-west Australia have been made for some years. Whitley (1946) describes an aerial survey (made in company with Mr. Stanley Fowler) in which an estimated 60,000 shoals of fish were observed. Reporting on these aerial observations in the area in May and June, Blackburn (1950, p. 244) states that, after a re-examination of the data collected by Whitley and Fowler, a minimum estimate of 10,000 shoals were seen, and that this is the greatest concentration of any fish seen from the air in Australian waters. These observations are of interest when considered in conjunction with the present work.

The surface pilchard off Starvation Boat Harbour were "thin" and gave no echogram. They could have been produced by pilchards at a density about the order of the drift net catches away from definite shoals, and it is considered that there was much less fish than occurred in the dispersed shoals where tuna were feeding between Albany and Doubtful I., which also gave no echograms; it is, however, the belief of the writer that dispersed subsurface shoals (such as occurred where tuna and birds were feeding) may constitute a quantity of fish equal to that where many shoals are recorded by the sounder. Until evidence to confirm this theory is produced, for practical purposes it must be assumed that a smaller quantity exists. It appears that some migration of pilchards occurs, as in the Culver Point region where the extensive surface fish occurred; *Warreen* log indicates a considerable area where no fish were seen and none caught.

In the New Zealand Queen Charlotte Sound pilchard fishery the shoal positions were shown on dark nights by peridinians (*Dinophysis*) and mysids, both of which were eaten by the pilchards. They caused intense phosphorescence in the water, and with practice fishermen were able to judge the size of the shoal by the intensity and area of the surface illumination and the depth to which it extended. The shoals came near to the surface at dusk, or after the moon had set on moonlight nights (Mishima 1951). A slight bump on the fishing vessel was sufficient to cause each fish in a shoal to give a sudden movement, which caused the phosphorescent organisms in the vicinity to light up. It is of interest also that the phosphorescent organisms disappeared in 1943 and the fishery was continued for a short time by the use of surface and submarine lights, but under these conditions became reduced to a bait fishery, and canning ceased.

Between Albany and Esperance 20 small samples of microplankton were taken with a ring net 7 in. in diameter of 150 meshes to the inch; phosphorescent organisms collected in this net represented an insignificant part of the plankton and little illumination of the surface was seen, but this means of locating surface shoals should not be overlooked.

VII. COMPARISON OF PILCHARD STOMACHS AND N70 TOW NET HAULS

The stomach contents of pilchards taken in ring and drift nets showed much digestion, and in all cases the food had been consumed some hours previously or even the day before.

Pilchards obtained from the drift net may have been caught several hours before death, but in the ring net only 60 min elapsed between capture and death. The similar stage of digestion suggests that food was taken the previous day. The data from these stomachs differ somewhat from those given in Table 5. Crustacea usually comprise 90 per cent. or more of the organisms present, but in one sample larval molluscs predominated and diatoms were also conspicuous; neither molluscs nor diatoms were obvious in pilchards from tuna stomachs (Table 5). Only once were Larvacea or Chaetognatha found; in fish caught by ring net they were small (*c.* 8 mm long) and comprised 7 per cent. of the organisms present. This suggests that pilchards may sometimes feed as a shoal, taking the organisms as they occur in the water. The predominance of copepods in N70 hauls and in the stomachs would indicate that this type of "grazing" frequently occurs, and the shoal may be able largely to retain its identity in feeding. As a full stomach in pilchards 160-170 mm long contains about 3 c.c. settled volume of organisms, the volume of water which a pilchard must graze to get a full feed can be calculated by comparison with N70 hauls. In Table 6 the volume of water required has been calculated on the assumption that an N70 net filters a cylinder of water 70 cm in diameter, 500 yd long. The volume of water required by a pilchard and

TABLE 5

PERCENTAGE OF DIFFERENT GROUPS OF ORGANISMS IN PILCHARD STOMACHS AND N70 TOW NETTINGS

Locality	Date of N70 Haul	Date of Stomach Collection	Copepods		Other Crustacea		Chaetognatha and Larvacea		Larval Molluscs		Other Forms	
			N70	Stomach	N70	Stomach	N70	Stomach	N70	Stomach	N70	Stomach
Entrance, King George Sound	12.v.51	18.v.51	95	85	2	9	—	4	—	—	3	2
Two People Bay	19.v.51	18.v.51	90	86	3	2	4	12	—	—	3	—
Cheyne I.	20.v.51	19.v.51	57	65	5	4	2	16	36	—	—	15
Cape Knob	20.v.51	20.v.51	66	87	2	5	10	5	19	—	3	3
Bremer Bay	24.v.51	5.vi.51	79	96	2	3	1	1	18	—	—	—
Cape Riche	10.vi.51	19.v.51	88	39	3	—	6	59	—	—	3	2
		Average	79	76	3	4	4	16	12	—	2	4

the distance necessary to travel as a shoal to obtain a full feed are also given. The distances given in metres in Table 6 vary from 2½ nautical miles at Cape Riche to 13½ nautical miles at Cheyne I. Small-shelled mollusc larvae show the greatest differences in stomach content and N70 tow-net haul. They are recorded for only three samples in Table 5, but were found to be widely distributed in net hauls of 150 meshes per inch. Swarms were probably taken in the localities given for N70 hauls. As none was eaten by any pilchards in the vicinity, it is suggested that the larval molluscs are consumed only in necessity and a pilchard shoal may be expected to move from an area where their normal food is scarce and molluscs or diatoms tend to dominate the plankton. From the distances given in Table 6, it is evident that pilchards roam over a considerable area to obtain sufficient food and this no doubt accounts for some of the migrations along the coast and in and out of bays.

TABLE 6

VOLUMES OF N70 HAULS AND PILCHARD STOMACHS* (EX TUNA STOMACHS) AND QUANTITIES OF WATER TO BE FILTERED TO OBTAIN A FULL STOMACH

Locality	Date of N70 Haul	Date of Stomach Collection	15-Min N70 Haul at 2 kt Settled Volume (c.c.)	Average Settled Volume Stomach Content (c.c.)	Volume of Water for Pilchards to "Filter" to Obtain 3 c.c. Feed (cu. m)	Distance Shoal of 75,000 Fish 9 m in dia. must Travel to Obtain a Full Feed (m)
Entrance, King George Sound	12.v.51	27.vi.51	88	1.5	12.0	14,100
Two People Bay	19.v.51	18.v.51	151	3.1	7.0	8,500
Cheyne I.	20.v.51	19.v.51	51	1.6	20.7	24,500
Cape Knob	20.v.51	20.v.51	165	3.0	6.4	7,500
Bremer Bay	23.v.51	5.vi.51	104	2.3	10.0	11,800
Cape Riche	10.vi.51	5.vi.51	340	1.2	3.1	4,700

* Six samples comprising 18 pilchards 160-170 mm long.

Pilchard stomach contents obtained from tuna stomachs were undigested, and the percentage of different types of organisms (calculated from the average number per microscope field) are given in Table 5. For comparison, N70 tow net hauls from the nearest locality are included. Copepods are still the dominant group, but mollusc larvae are completely absent. Chaetognatha and Larvacea occur in the stomachs in greater proportion than in the tow net hauls and, although it is obvious that the tow net may not catch these more active organisms very efficiently, it is clear that unless they are actively hunted they may also avoid capture by pilchards. The chaetognaths in these stomachs also were larger than in fish caught by ring net, measuring 8-12 mm long. It appears that tuna (*Thunnus maccoyii* Castlenau) catch only the actively feeding pilchards, and it is suggested that when feeding conditions are good the pilchard shoals break up in order to obtain food more readily, and this makes them easier prey for tuna.

VIII. QUANTITY OF PILCHARDS—ALBANY TO ESPERANCE

In Table 7 the data from the echo-sounder record are tabulated. The weight of fish per shoal has been estimated on the basis that shoals 10, 36, and 42 ft in diameter produce respectively 200 lb, 3 tons, and 8 tons, which give densities of 1 lb of fish to 2.62, 3.62, and 3.58 cu. ft of water. Estimates have been made on the average of 1 lb of fish per 3.3 cu. ft of water. The width of track surveyed by the sounder is given according to the size of the shoal (see footnote on p. 236) and the quantity per acre and per square nautical mile calculated from this (on the basis of 850 ac per sq. nautical mile).

TABLE 7

SUMMARY OF DATA ON PILCHARD SHOALS FROM ECHOGRAMS, ALBANY TO ESPERANCE, MAY-JUNE 1951

Locality	Miles Travelled	Shoals per Mile	Average Diameter (ft)	Width of Track Surveyed (ft)	No. of Shoals per Acre	Quantity of Pilchards		
						per Shoal (lb)	per Acre (lb)	Nautical (tons) Mile per Sq.
Albany	92	1.1	19	32	0.24	1080	259	98
Two People Bay	5	1.6	17	30	0.37	780	288	111
Bremer Bay	63	0.4	26	39	0.07	2790	195	76
Doubtful Bay	6	1.7	10	23	0.52	158	82	15
Esperance Bay	10	3.9	12	25	1.10	274	301	114
Mississippi Bay	14	0.2	12	25	0.06	274	16	6

From Albany to Doubtful I. the area of water under 30 fm, where the best echograms of pilchards were made, comprises about 265 sq. nautical miles, and taking an average of 75 tons per mile the total quantity estimated from the sounder in this area is 19,800 tons. In Esperance Bay, in the 65 sq. miles where pilchards showed on the sounder, the quantity at 114 tons per sq. mile is 7410 tons. The data for the extensive area between Doubtful I. and Esperance, about 490 sq. miles under 30 fm, are insufficient for any reliable estimate. East of Doubtful I. 15 tons per sq. mile and near Esperance only 6 tons were found, and no shoals were recorded on the echo-sounder for several miles off Starvation Boat Harbour, which indicates a relatively small quantity.

The quantities of pilchards given above represent the fish in shoals actually available for ring netting at the time the records were made. The total quantity of pilchards 150-180 mm long will be greater than this as the shoals appear to form and disperse fairly frequently. It is reasonably certain that the total quantity will not be many times the amount calculated from the sounder record but it may be several times, and twice the quantity is suggested as a good working hypothesis for the total available supplies.

IX. CONCLUSIONS

In conclusion, it may be said that, although the ring net used in conjunction with the echo-sounder on the *Warreen* was not entirely successful, the results give promise of a pilchard fishery in south-west Australia. In the course of the work by *Warreen* in 1951, no definite information on the reason for the appearance on the surface or quietness of shoals was obtained, but of the eight hauls recorded, catches were made when barometric pressure was over 30.0 in., and there was no catch when the pressure was less than 30.0 in. This may be simply related to the weather, which is unsettled in the autumn, gales alternating with short periods of fine weather.

The difficulty of estimating the quantity of fish available from the "misleading surface display" so frequently described (Blackburn 1950; Blackburn and Rayner 1951; Whitley 1946), led the writer to make estimates of the quantities of pilchards which may be present in the area surveyed by echo-sounder. Thompson (1943), writing on the productivity of Australian waters, states that no single species of fish is likely to produce more than 5000 tons per annum and, although for some species slightly more than this quantity has been caught, the order of magnitude will not be exceeded unless some improved methods are developed. Pilchards are probably the most abundant species in south-west Australia, and detection by echo-sounder may be the initial step in developing this industry. The use of lights for night fishing after locating shoals is worth further trial in this area; the small size of the shoals, however, suggests that ring nets of fine twine which may be hauled quickly have good prospects of success.

X. ACKNOWLEDGMENTS

The writer is indebted to Mr. G. W. Rayner for assistance in the early stages of the work, and to Dr. M. Blackburn for biological data. Captain C. Pedersen, Master of the *Warreen*, was mainly responsible for carrying out the work at sea. Dr. H. Thompson, Chief of the Division of Fisheries, encouraged the author to develop the method of calculating the quantities of fish in shoals.

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APPENDIX I

ECHO-SOUNDER RECORD OF PILCHARD SHOALS: ALBANY TO ESPERANCE, 1951

Date	Locality	Distance Travelled (miles)	No. of Shoals	Shoals per Mile	Time (hr)
May 11	King George Sound	27	38	1.41	9
13	King George Sound	12	27	2.25	4
14	King George Sound	9	6	0.67	3
17	King George Sound	20	17	0.85	6½
18	King George Sound to Two People Bay	9	9	1.0	3
19	Two People Bay to Cape Riche	30	14	0.46	5
20	Cape Riche to Dillon Bay	50	53	1.06	8⅓
23	Bremer Bay	27	6	0.22	9
24	Bremer Bay to Doubtful I. Bay	36	20	0.55	6
25	Doubtful I. Bay to Starvation Boat Hbr.	57	26	0.46	9½
27	Starvation Boat Hbr. to Albany	60	8		20
June 3	King George Sound to Cape Vancouver	24	15	0.63	7¾
4	King George Sound to Two People Bay	42	10	0.24	7
5	Two People Bay to Cape Riche	57	17	0.32	9½
6	Cape Riche to Dillon Bay	48	6	0	8½
	Dillon Bay		6		
8	Dillon Bay	24	24	1.0	8½
9	Dillon Bay	42	22	0.52	7½
11	Doubtful I. Bay to Fanny's Cove		Too much roll		
12	Fanny's Cove to Esperance	27	2	0.08	4½
	Bay	1	6	6.0	¼
	Esperance Bay	9	33	3.7	1½
13	Esperance Bay to Lucky Bay	12	4	0.33	2
14	Lucky Bay		0	0	1
	Mississippi Bay	6	17	2.8	1
	Mississippi Bay	8	5	0.63	2
	Mississippi Bay to Sandy Hook	35	45	1.3	5¾
15	Sandy Hook		0	0	1
	Esperance Bay	12	38	3.2	3
16	Esperance Bay	3	17	5.7	½
	Esperance Bay to Red I.	12	27	2.25	2
	Red I. to off Fanny's Cove	15	6	0.4	2½
19	Dillon Bay to Cape Riche	26	1	0.05	5
	Cape Riche to Bold I.	25	17	0.7	4
	Bold I. to Two People Bay	14	16	1.1	2¼

PILCHARD SHOALS IN SOUTH-WEST AUSTRALIA

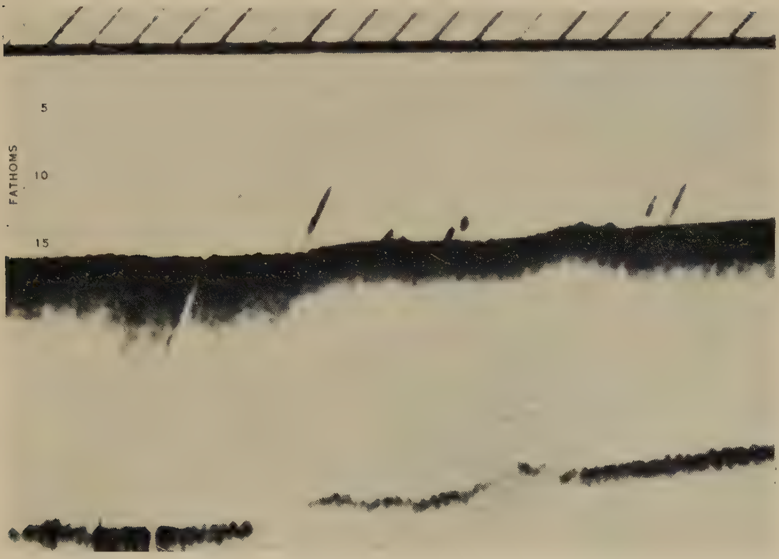


Fig. 1.—Echogram of eight pilchard shoals, Esperance Bay, 1.30-1.45 p.m. June 13, 1951.

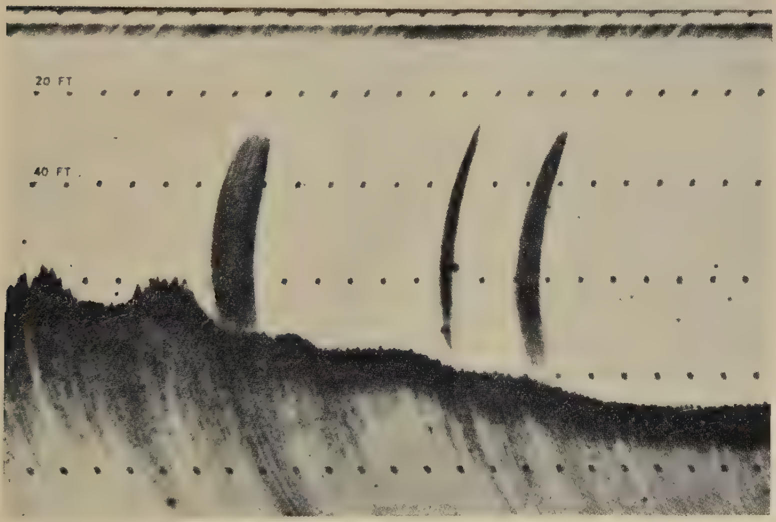


Fig. 2.—Isolated pilchard shoals off the Cornish coast (from Hodgson 1950, p. 12, Fig. 6).

PILCHARD SHOALS IN SOUTH-WEST AUSTRALIA

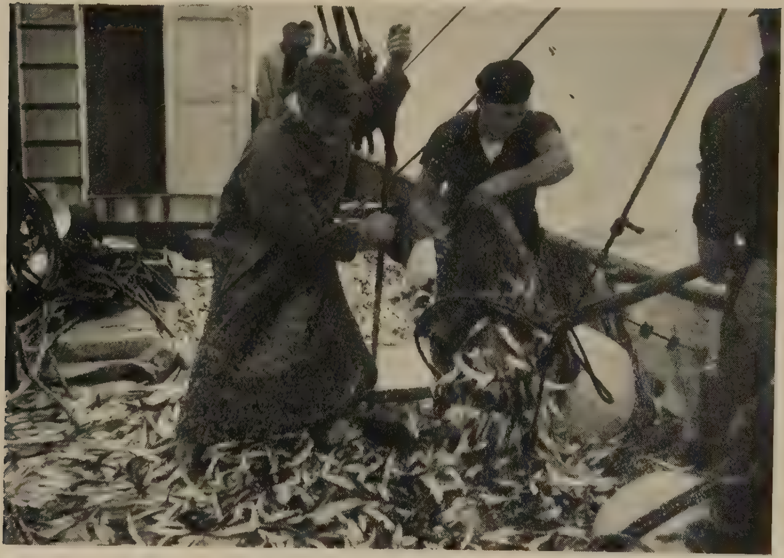


Fig. 1.—Brailing pilchards from ring net on to deck of *Warreen*.

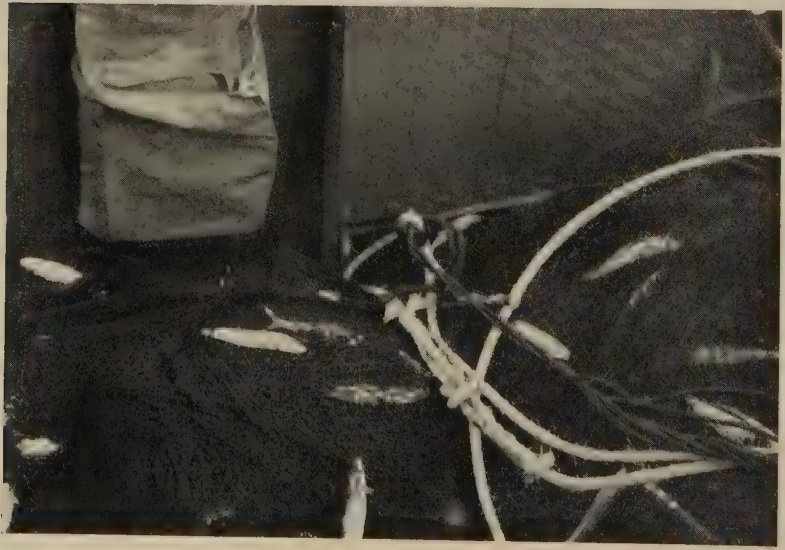
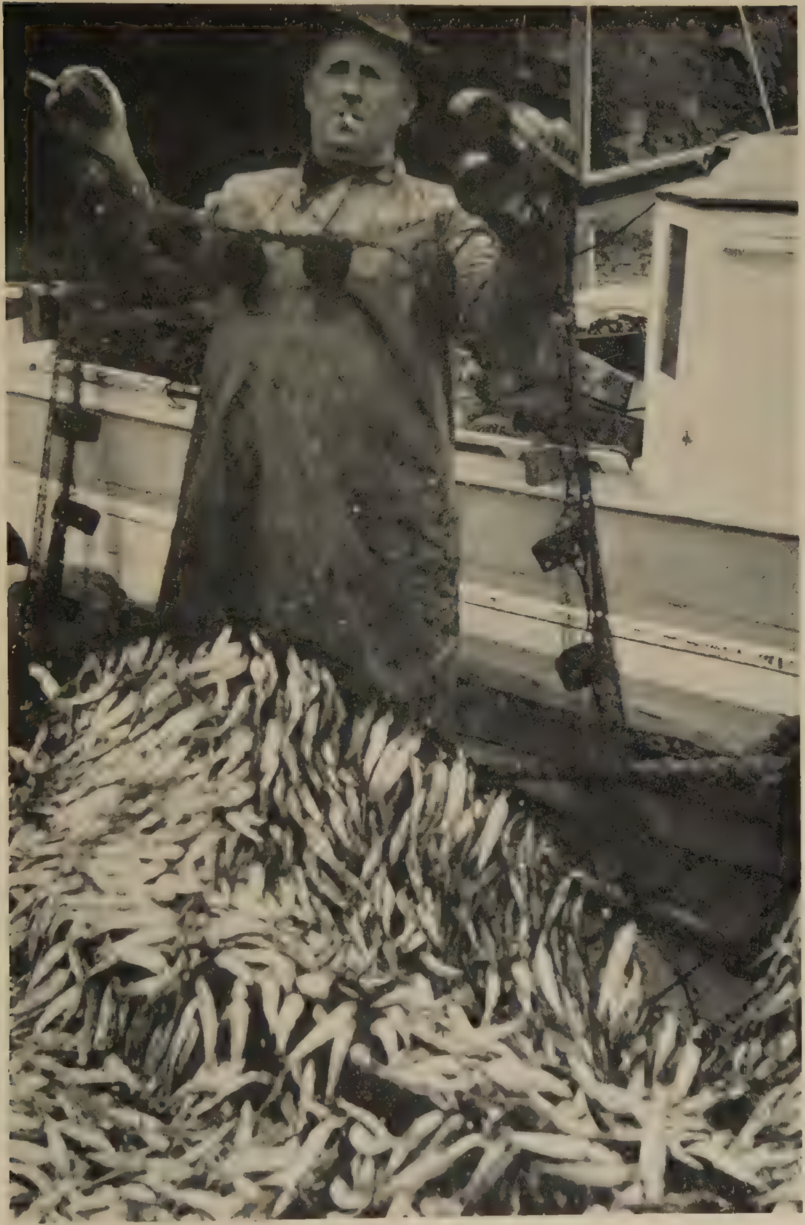


Fig. 2.—Meshed fish caught in a drift net.

PILCHARD SHOALS IN SOUTH-WEST AUSTRALIA



Meshed fish caught in a ring net.

FURTHER RESULTS OF TAGGING SEA MULLET, *MUGIL CEPHALUS* LINNAEUS, ON THE EASTERN AUSTRALIAN COAST

By G. L. Kesteven*

(*Manuscript received May* 25, 1953)

Summary

An account is given of tagging operations in eastern Australian waters on sea mullet. The operations involved fish of wide age and size ranges in a variety of habitats and localities, in all months of the year except July. The recoveries from these operations are analysed for information on movement, growth, and mortality.

The results show the movement of the tagged fish to be predominantly northwards and require a postulate that southward movement takes place among the young fish (and possibly eggs). The movement of individual fish can be quite rapid and cover long distances, and each fish probably migrates a number of times during its lifetime. The proportion of the population involved in these movements probably exceeds 50 per cent.

The results show that there is on the coast one continuous stock of this species, of which the populations occupying the numerous rivers and lakes constantly intermingle.

Confirmation was obtained of the earlier work on the technique of scale reading in this species, and of the general results on average growth rate. Growth occurs chiefly in summer, but possibly also in the latter part of spring and the early part of autumn. The physiology of scale growth and the formation of annual "breaks" are discussed.

Proportional recoveries from each operation are reported but these cannot serve well as an index of intensity of fishing. On the other hand, the longevity of the tags serves to indicate the probable life expectancy of these groups of fish; this is estimated as slightly more than 3 yr.

I. INTRODUCTION

A brief account (Kesteven 1942) has been given of tagging operations in relation to the biology of the principal Australian species of mullet, *Mugil cephalus* Linnaeus (= *M. dobula* Günther). A total of 2722 releases and 74 recoveries was reported.

This preliminary work permitted only tentative conclusions, as follows:

(*a*) Fishing intensity and growth rate could not be judged from results.

(*b*) Tagging results proved quite conclusively that the river mullet and sea mullet were one and the same species, being distinct life phases.

(*c*) The movement of mature fish was mainly northwards.

(*d*) Individual mullet could make lengthy migrations, but the length of migration varied considerably between individuals.

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(*e*) Movement took place chiefly in autumn.

(*f*) It was difficult to estimate the proportion of stock which moved in each year.

There have since been further releases and recoveries and the results of this later work lead to some extension and modification of the above conclusions. At the same time the results indicate that the programme in this form should be regarded as complete and that a distinct change should be made in the plan of future work. Accordingly the results of this work to date are reported and certain conclusions are drawn, including an indication of the course which further work should take.

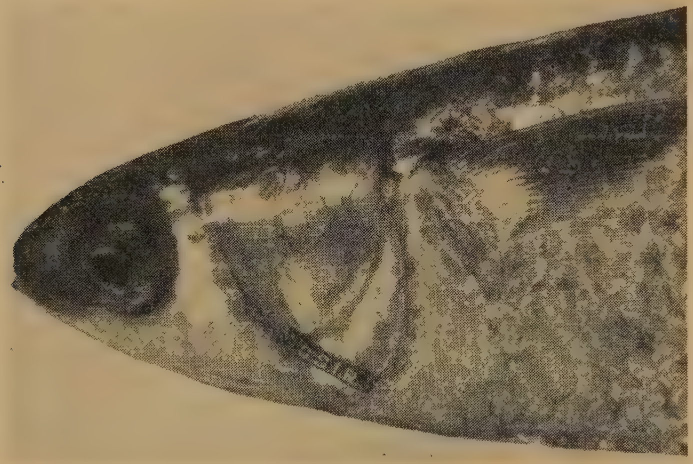

Fig. 1.—Tag affixed to the gill cover of a mullet.

II. METHODS

A metal (German silver) opercular tag was used, bearing the letters C.S.I.R. and a serial number. It was attached with special pliers. The tag, pliers, and a tag in position are shown (Fig. 1; Plate 1, Fig. 1).

Tagging was in general carried out during field expeditions conducted for general biological purposes.

All fish for the experiments were caught by professional fishermen, generally operating beach seine gear. Some supplies were provided by meshing gear, but since the losses by fatal damage to the fish were so great in this method it was used only occasionally when no other was available.

The tagging team generally consisted of three members: one recording clerk who also handled the scale envelopes, one to measure the fish and hold it for tagging, and one to carry out the actual tagging operation and to remove a few scales.

Care was taken during tagging to avoid damage to the gills and to the blood vessels lying on the inner face of the gill cover. Scales were removed from a position a few centimetres behind the pectoral fin. Despite care some fish were injured so badly that they appeared unlikely to survive; in a few it was possible to recover the tag at once and strike the number from the lists. A few fish were released without measurement or without a scale sample being taken.

Certain recoveries were made in Port Hacking by the laboratory staff, and a few came from markets, but the majority were made by fishermen during commercial operations. Publicity was given to the project and the assistance of fishermen was sought. A reward was offered for returned tags, yet there was, we believe, some neglect not only in searching for tags, but also in returning recovered tags.

III. RELEASES

Table 1 lists all releases made during the recent work and those reported earlier (Kesteven 1942), but not those made with metal strap and celluloid strip; 4125 releases are listed, but a little doubt exists about the status of a few releases where the fish were damaged. There were 60 separate tagging operations with an average number of about 69 releases.

TABLE 1

TAGGING OPERATIONS

Operation* No.	Date	Locality	Nos.†	No. of Fish
30	5.v.39	Ballina, Richmond River	801-846	45
20	5.v.39	Ballina, Richmond River	848-880	31
21	9.xi.39	Gunnamatta Bay, Port Hacking	881-1172	155
22	16.xii.39	Nicholson River	1601-1620	19
23	8.ii.40	Ulmarra, Clarence River	1402-1533	132
24	13.v.40	Gunnamatta Bay, Port Hacking	1534-1712	158
25	20.vi.40	Entrance to Weyba Lake, Noosa		
26	11.i.41	River	1713-1804	91
		Entrance to Noosa River	1805-1914	109
27	21.vi.40	Entrance to Noosa River	1915-1949	35
28	21.vi.40	Greenwell Point	1950-1994	45
29	10.i.41	Lake Illawarra	1995-2296	102
31	24.ii.41	Port Hacking	2401-2591	191
32	19.iii.41	Hawkesbury River	2297-2306, 2592-2600	19
33	20.iii.41	Lake Macquarie	2307-2400, 2416, 2601-2700	195
34	4.v.41	Clarence River	2801-2818	18
35	6.v.41	Richmond River	2715-2748	34
36	7.v.41	Tweed River	2749-2761	13
37	8.v.41	Terranora Creek	2762-2784	23
38	11.v.41	Noosa River	2785-2825	23
39	15.v.41	Terranora Creek	2826-2925	100
40	16.v.41	Currumbin Creek	2926-3126	202
41	1.xii.41	Port Hacking	3127-3211	85

TABLE 1 (*Continued*)

Operation* No.	Date	Locality	Nos.†	No. of Fish
42	28.v.42	Port Hacking	1-50	50
43	30.v.42	Port Macquarie	51-62	12
44	31.v.42	Port Macquarie	63-90	28
45	1.vi.42	Port Macquarie	91-126	35
46	25.vi.42	Port Hacking	127-341	214
47	29.x.42	Gunnamatta Bay, Port Hacking	342-379	38
48	5.i.43	Fisherman's Bay, Port Hacking	380-400, 4001-4188	209
49	3.ii.43	Sand spit, Port Hacking	308, 4021, 3212-3272, 4076, 4104	65
50	4.ii.43	Sand spit, Port Hacking	171, 361, 3273-3400, 4189-4200	142
51	19.iii.43	Gunnamatta Bay, Port Hacking	2300, 3398, 4201-4322	124
52	8.iv.43	Fisherman's Bay, Port Hacking	270, 4125, 4127, 4169, 4177, 4175, 4323-4425	109
53	15.iv.43	Gunnamatta Bay, Port Hacking	4428-4500	73
54	14.ix.43	Fisherman's Bay, Port Hacking	501-650, 3214, 4095, 4177, 4238, 4368	155
55	11.x.43	Fisherman's Bay, Port Hacking	509, 651-800, 3214, 3307, 4121	154
56	8.vi.43	Bribie Passage, 9 miles SW. of Caloundra	4501-4515	15
57	18.viii.43	Near Mitchell's boatshed, Southport beach	4516-4536, 4689-4700	33
58	2.xi.43	Nerang River, Southport	4537-4610, 4693, 4694	76
59	2.xi.43	Near Mitchell's boatshed, Southport beach	4681-4688	8
60	9.xi.43	Reedy I., Nerang River, Southport	4611-4680	70
				3435

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* Operations 1-19 were made with an unsatisfactory tag and are neglected.

† Discrepancies between the number of tags indicated and the number of fish released, e.g. operation 22, are due to losses of tags.

Releases were made at localities as widely separated as the Nicholson River, Vic., and the Noosa River, Queensland, a distance of 1000 miles. Figure 2 shows the tagging localities.

The greatest number of releases and operations was at Port Hacking, viz. 1936 fish in 14 operations (56.4 per cent. of releases in 23.3 per cent.

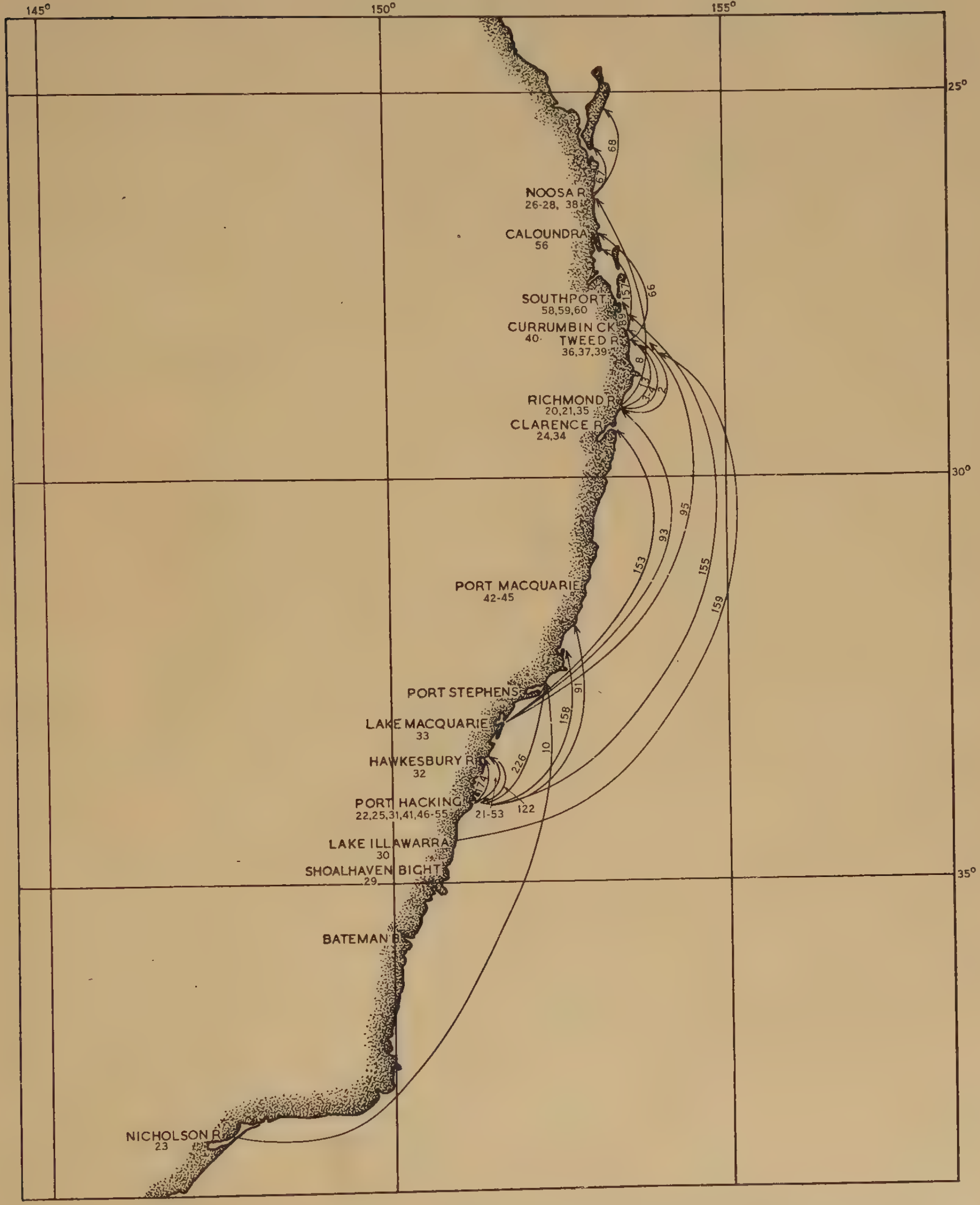

145°
150°
155°
25°
30°
35°
68
67
NOOSA R.
26-28, 38
CALOUNDRA
56
66
157
SOUTHPORT
58,59,60
89
CURRUMBIN CK
40
TWEED R
36,37,39
8
2
RICHMOND R
20,21,35
CLARENCE R
24,34
95
93
153
155
159
PORT MACQUARIE
42-45
16
91
PORT STEPHENS
158
LAKE MACQUARIE
33
10
226
HAWKESBURY R
32
174
PORT HACKING
22,25,31,41,46-55
21-53
122
LAKE ILLAWARRA
30
SHOALHAVEN BIGHT
29
BATEMAN B
NICHOLSON R
23

Fig. 2.—Tagging localities listed in Table 1 and the paths taken by fish which moved from their locality of release. The small numbers on the line showing the path of movement refer to the tag recovery number (Appendix I).

of operations, with an average of 138.2 per operation, compared with 32.6 for the other 46 operations, and with 57.6 for all operations). Port Hacking is an invaded estuary with waters generally of fairly high chlorinity, there being only a small freshwater contribution except during the infrequent floods. The Port Hacking River is a short, shallow stream, principally a storm water channel, running through Hawkesbury sandstone. During most of the year the greater part of its course is a rocky bed receiving some seepage from the surrounding hill slopes. A short section of the river carries fresh water continuously and is closed off from the estuary by a weir about 4 miles from the coast; the flow of water over this weir is small. The estuary itself (Fig. 3) is generally shallow; a narrow channel leads up the estuary and into each arm, and there are a few deep holes, but there are wide expanses of shallow bottom exposed at low tide. The bottom varies from pure sand at the sea end to mud near the weir, but most of the intertidal flats are composed of muddy sand with a fair proportion of shell. The intertidal flats carry a fairly heavy biota, with a variable flora of *Zostera* and *Posidonia* and a dense molluscan and worm fauna. Where small streams enter the estuary there is a slight delta formation with a heavier proportion of mud and a sparse growth of mangrove.

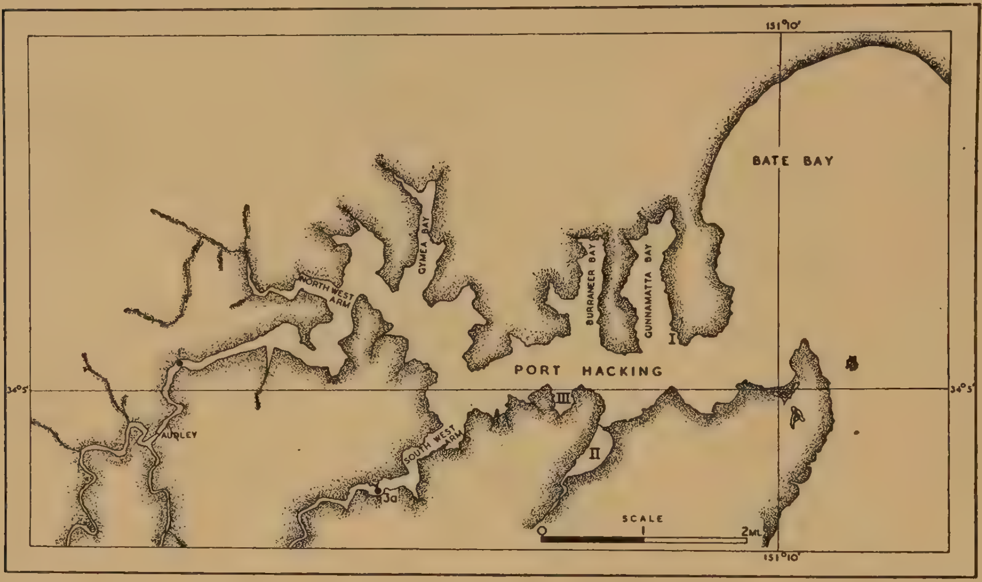


Fig. 3.—Port Hacking, showing tagging localities.

Tagging took place wherever the opportunity offered; most of the operations were near the sea, on the flat at the entrance to Gunnamatta Bay ("I" in Fig. 3), some on Fisherman's Bay (III) (ecologically a similar location), some in Cabbage-tree Creek (II), and some much further up the estuary. Table 2 gives temperature-chlorinity data on the estuary for the times at which tagging operations took place.

A few of the releases, including those of operations 1, 20, and 21, were of fish moving in the sea. Many were of fish lying immediately inside the estuary in water of nearly sea-water salinity, others were of fish in brackish water, and a few of fish in practically fresh water. The releases are classified ecologically in Table 3.

TABLE 2

TEMPERATURE AND CHLORINITY IN PORT HACKING (MOUTH OF GUNNAMATTA BAY) AT THE TIME OF TAGGING OPERATIONS

Tagging Operation		Temperature and Chlorinity	
Date	No.	Surface Temperature (°C)	Surface Chlorinity (Cl°/00)
9.xi.39	22	—	—
13.v.40	25	18.50	19.25
10.ii.41	31	23.40	19.34
1.xii.41	41	20.40	19.63
25.vi.42	46	15.50	19.25
29.x.42	47	17.50	17.26
5.i.43	48	19.10	19.45
3.ii.43	49	22.80	19.71
4.ii.43	50	22.80	19.71
19.iii.43	51	24.50	19.90
8.iv.43	52	21.85	19.59
15.iv.43	53	20.60	19.74
14.ix.43	54	14.50	19.43
11.x.43	55	17.25	19.13

TABLE 3

ECOLOGICAL CLASSIFICATION OF TAGGING OPERATIONS

Sea-water	Marine Zone of Estuary	Brackish Water	Fresh or Nearly Fresh Water
20, 21, 26	22, 25, 27, 28, 29, 30, 31, 33, 34, 35, 36, 38, 40, 41, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60	32, 37, 39, 42, 43, 44, 45	23, 24

Operations were carried out in every month of the year except July; the operations can, however, be more properly considered in relation to season and to a division of the year according to the habit of the mullet, into periods of sea-movement and of river life. These periods vary in relation to the calendar year from point to point along the coast; there is also some variation from year to year. Catches of travelling fish can be made on the south coast of New South Wales in early February-April, on the north coast in March-May, and in southern Queensland in April-June. A grouping of the tagging operations according to season and biological division of the year is given in Table 4.

TABLE 4

CLASSIFICATION OF TAGGING OPERATIONS BY BEHAVIOURAL CHARACTERISTICS OF THE FISH

Awaiting Migration	Migrating	Dispersed
26, 27, 28, 34, 35, 36, 37, 38, 39, 40, 52, 53	20, 21	22*, 23, 24, 25, 29, 30, 31, 32, 33, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 54, 55, 57, 58, 59, 60, 56

* This lot might have assembled as a preliminary to a "hardgut" migration.

The lengths (snout to caudal fork) of released fish ranged from 16.6 to 51.2 cm, with the majority 25-35 cm. The releases included fish from I to at least VI in age. Table 5 gives an analysis of the size and age composition of the groups of fish released.

Table 6 summarizes the foregoing information on these releases, combining Tables 3, 4, and 5. Certain of the vacant compartments in this table cannot normally become filled; thus fish migrating or schooled awaiting migration are not found in fresh water, and dispersed fish are not found in sea-water. Schooled fish travelling down a river or across a lake towards the sea could no doubt be captured and tagged, but no such captures were made in this work.

IV. RECOVERIES

The recoveries from these operations (including those reported in the earlier paper) are listed in Appendix I and summarized in Table 7. The overall return was 6.4 per cent. (224 recoveries from 3435 releases), but varied between nil and 26.2 per cent. for different operations. This variation is discussed in the hope of giving guidance to the conduct of similar operations in the future.

The work was intended to give quantitative information on:

(*a*) Migrations,
(*b*) Growth rate,
(*c*) Mortality (natural; fishing).

Migration, where it occurred, is indicated by the distance travelled and direction of travel; growth is given by the change in size of the fish, which may be supplemented by information from scales; and mortality in

TABLE 5

SIZE AND AGE COMPOSITION OF GROUPS OF FISH RELEASED

Operation No.	No. Released	Size (L.C.F. in cm)			Age*					
		Largest	Smallest	Mean	I+	II+	III+	IV+	V+	VI+
20	45	58.2	34.9	40.87	—	—	—	—	—	—
21	31	54.7	39.6	45.24	—	—	—	—	—	—
22	155	37.5	22.0	27.80	92	68	20	4	—	—
23	19	46.5	32.5	35.70	—	1	15	3	—	—
24	132	42.5	24.0	30.20	1	108	13	6	—	1
25	158	39.9	25.0	30.56	66	77	3	—	—	—
26	91	42.2	30.7	35.99	—	—	—	—	—	—
27	109	44.7	31.4	39.20	—	—	—	—	—	—
28	35	41.2	30.9	34.27	—	—	—	—	—	—
29	45	31.1	20.2	26.36	1	22	21	—	—	—
30	102	31.8	20.2	25.11	91	2	—	—	—	—
31	191	38.3	22.3	28.62	30	96	49	3	1	—
32	19	34.9	18.8	21.31	—	—	—	—	—	—
33	195	40.5	24.9	32.04	—	32	111	34	—	—
34	18	28.7	23.2	25.16	15	3	—	—	—	—
35	34	42.5	20.3	31.60	7	6	12	2	—	—
36	13	34.5	19.7	25.57	5	3	2	—	—	—
37	23	39.8	26.0	32.93	1	10	9	1	—	—
38	23	48.2	25.0	33.56	—	—	—	—	—	—
39	100	32.5	19.9	23.39	65	15	—	—	—	—
40	202	42.5	17.8	23.46	159	23	—	—	—	—
41	85	35.7	22.5	27.55	32	42	7	—	—	—
42	50	33.5	18.2	25.61	—	—	—	—	—	—
43	12	38.2	25.3	30.66	4	6	1	—	—	—
44	28	31.5	16.5	24.25	15	7	—	—	—	—
45	35	25.6	16.8	22.18	26	1	—	—	—	—
46	214	35.9	19.6	28.22	47	125	18	—	—	—
47	38	33.4	23.0	29.66	4	23	7	—	—	—
48	209	38.7	22.9	31.75	—	50	114	5	—	—
49	65	37.0	26.7	31.45	—	16	34	—	—	—
50	142	35.7	23.4	30.27	—	—	—	—	—	—
51	124	40.5	16.8	33.64	3	4	71	27	3	—
52	109	35.5	21.9	27.49	9	52	16	—	—	—
53	73	39.4	33.8	36.56	—	—	12	42	3	—
54	155	35.2	22.5	30.31	20	89	31	5	—	—
55	154	36.0	24.0	30.77	24	64	43	4	—	—
56	15	39.8	20.5	28.83	5	5	1	1	—	—
57	33	28.1	19.1	23.63	23	3	—	—	—	—
58	76	27.3	18.0	21.64	16	49	11	—	—	—
59	8	23.2	20.0	21.90	2	4	—	—	—	—
60	70	21.5	18.5	20.49	6	59	—	—	—	—

* Owing to failure to collect scales at release, age analyses are unavailable for some releases. Failure to collect scales and unreadability of scales account for discrepancies between numbers released and numbers for which age was read.

each operation is represented by the total "life" of the recovered tags, and the proportion of liberated tags recovered. Each of these could presumably be given an appropriate score and a total score could be obtained for each operation. However, both "no growth" and "no migration" are, under certain circumstances, the full possible information and it is difficult to see how this could be scored equally with considerable growth and extended migration.

TABLE 6

FISH OF EACH AGE RELEASED IN EACH PHASE AND EACH ECOLOGICAL AREA

Total numbers of fish liberated in each ecologico-behavioural situation are given in brackets, and numbers of released fish from which readable scales were taken are given without brackets. No scales were taken from migrating fish

Habitat	Age	Behavioural Characteristic								
		Awaiting Migration			Dispersed			Totals		
Sea-water	I+	—			—			—		
	II+		—			—			—	
	III+			—			—			—
	Total			—			—	(91+76*)		—
		(91)						(167)		
Marine zone of estuary	I+	195			462			657		
	II+		87			821			908	
	III+			89			697			786
	Total			371			1980			2351
		(768)			(2065)			(2833)		
Brackish zone of estuary	I+	66			45			111		
	II+		25			14			39	
	III+			10			1			11
	Total			101			60			161
		(123)			(144)			(267)		
Fresh or nearly fresh water	I+	—			1			1		
	II+		—			108			108	
	III+			—			38			38
	Total			—			147			147
		—			(151)			(151)		
Totals		261	112	99	508	943	736	769	1055	835
		(982)		472	(2360)		2187	(3342)		2659

* In operations 20 and 21, 76 fish were released in sea-water when actually engaged in migration.

On the other hand, the "life" of a tag is both a simple figure to handle and a valuable indication of the amount of information available from the return; it is obvious that the longer a tagged fish remained free the greater would be its chances of having grown appreciably and accomplished notable migration. Simply stated, an "older" tag is likely to provide more information. In comparing individual operations, the greater the number of recoveries and the greater their age the more informative the operation.

In Table 7, columns 4 and 6 give the recovery proportions and the average "life" of each operation. Recovery proportion may theoretically take any value between 0 and 100 per cent.; but in practice it is inconceivable that it could reach 100 per cent., and the hope is that it should approximate to the rate of exploitation for the stock into which the tags have been released (which is, however, a figure which the operations are planned to reveal). If the true rate of exploitation were known the recovery proportion could be expressed as a percentage of this; deviations below or above 100 would then be counted as measures of experimental defect in adjusting the results to conform to the other sets of information from the operation.

No estimate of the true value of the rate of exploitation is available but it may reasonably be assumed on experience from other fisheries that it would exceed 30 per cent., and since the recovery rates from these operations are all less than 30 per cent. it seems reasonable to use them as they stand as an index of the success of each operation regarding the information it gives on fishing intensity. Reasons are given below for believing that the recovery proportions given in Table 7 do not correspond to the true exploitation rates of the stocks into which the tags were released, but are probably low. To use the recovery figure without adjustment would be in effect to reckon the greatest recorded proportion as the true rate; but even if the true rate were greater than this, as we believe, these proportions although all overvalued would still hold the same relative positions, and therefore the present procedure could be regarded as indicating relative success; if, however, the true rate were less than the greatest recorded in Table 7, then some would be overvalued and some undervalued, and the relative positions would be wrong; at this stage it is assumed that this has not happened.

However, the recovery proportion is not by itself an adequate index of the value of an operation, for obviously two operations with equal recovery proportions but different average "life" of recovered tags would be of different values; similarly 100 per cent. recovery after a few days undoubtedly would be less informative than 1 per cent. recovery after many days. Greater duration of freedom of tagged fish is likely not only to be more in accordance with what occurs in nature, but also to carry more information about each fish. Therefore average "life" of recovered tags must also be considered. However, the operations vary in ranking according to these two indices, operation 49 being most successful in recovery proportion whilst operation 30 has the highest average "life". The question then is how to combine these indices into a single index of success. For this purpose we have treated the figures of columns 4 and 6 of Table 7 as indicating the value of each operation in the two respects discussed, and multiplied them together, the product being given in column 7. It will be observed that this new index (B) equals $p \times t = r/R \times T/r = T/R =$ average number of days of freedom per liberated tag.

TABLE 7
RESULTS OF TAGGING OPERATIONS

1. Operation No.	2. No. Released (R)	3. No. Recovered (r)	4. Recovery Proportion (%) (p)	5. Total Days of Freedom (T)	6. Average Days of Freedom (t)	7. Index of Success (B)
20	45	4	8.9	1063	266	23.62
21	31	3	9.7	91	30	2.94
22	155	2	1.3	622	311	4.01
23	19	2	10.5	241	121	12.68
24	132	4	3.2	196	49	1.48
25	158	32	20.2	4054	127	25.65
26	91	6	6.6	1464	244	16.09
27	109	(7)* 6	6.4	570	95	5.23
28	35	1	2.9	356	356	10.17
29	45	—	—	—	—	—
30	102	(5)* 4	4.9	2330	583	22.84
31	191	2	1.6	690	345	3.61
32	19	2	10.5	752	376	39.58
33	195	5	2.6	1638	328	8.40
34	18	—	—	—	—	—
35	34	2	5.9	277	139	8.15
36	13	—	—	—	—	—
37	23	(3)* 2	13.0	78	39	3.39
38	23	2	8.7	153	77	6.65
39	100	13	13.0	2034	156	20.34
40	202	6	3.0	2923	487	14.47
41	85	1	1.2	86	86	1.01
42	50	1	2.0	531	531	10.62
43	12	1	8.3	231	231	19.25
44	28	—	—	—	—	—
45	35	—	—	—	—	—
46	214	9	4.2	1700	189	7.94
47	38	2	5.3	140	70	3.68
48	209	23	11.0	4333	188	20.73
49	65	17	26.2	1293	76	19.89
50	142	4	2.8	517	129	3.64
51	124	12	9.7	2803	234	22.61
52	109	20	18.4	2984	149	27.38
53	73	5	6.9	591	118	8.10
54	155	11	7.1	3300	300	21.29
55	154	9	5.8	2923	325	18.98
56	15	—	—	—	—	—
57	33	5	15.2	525	105	15.91
58	76	3	4.0	465	155	6.12
59	8	—	—	—	—	—
60	70	—	—	—	—	—
Totals	3435	(224) 221		41,954		
Average			6.5		190†	12.21

* The figures in brackets refer to the number of tags recovered; in each case one tag was returned with no data as to time, place, etc., of recovery; the calculation of "t" excludes the no-information tag.

† The geometric mean for this is 158 days.

This aspect need not be elaborated, but it may be pointed out that whilst the figure is not a real one so far as the biology of the fish is concerned, it is real as far as the operations are concerned, since it is calculated from the total days of freedom recorded and the number of tags released, and the former is dependent upon the factors which determine the number of tags recovered and their "life". The index is not to be thought of as representing the average life of the fish of the population into which the tags have been released, or even of the liberated tags. Where the recovery proportion corresponded exactly with the rate of exploitation the index would be in approximately the same ratio to the true "life" of liberated tags as recovered tags to tags liberated. Probably a mathematically more acceptable means of combining the two indices could be devised, such as adding together some function of each representing external measures of the factors influencing recovery and "life", but further elaboration of the treatment of the present series of data is not warranted.

In Table 7 the results of the operations are set out in chronological order; the results may also be grouped according to the classifications given in Tables 3 and 4, and according to the number of tags released, so that operation 59 would stand first with 8 tags released and operation 46 last with 214 tags released. In such regroupings the values of p, t, and B for each operation may be marked according to whether they fall below or above the average value. (A geometric mean was taken for t because of the skew nature of the distribution.) The number of better than average results may then be tallied for each category for each index; the results are shown in Table 8.

For each of the parts of Table 8 an estimate of the number of better than average results for each category has been made on the assumption that, if the circumstances relating to each category exercised no influence, each category would have a proportion of the total number of better than average results roughly equal to its proportion of all operations. These estimated figures are given in brackets. Owing to the generally small numbers it is not possible to apply the χ^2 test to parts (i) and (ii) of this table, but the figures indicate that probably neither the locality of operation nor the bionomic status of the fish exercised any influence on the results. Similarly the proportion of return (p) is apparently not affected by numbers released (part (iii)), but for t and B there are moderately significant departures from the estimated values. Considering the small numbers of recoveries from all experiments, the result in Table 8(iii) suggests that, whilst entirely random factors determine whether *any* recovery is obtained from an experiment and if the release numbers are too low there may be no recovery, if the releases are of sufficiently large number the chances of late recoveries are greater. The 16 operations with releases less than 40 include six from which there was no recovery, and the 21 operations with less than 70 include eight. In addition, although there are exceptional operations, there is a positive regression of average duration of freedom on number of tags released. These results indicate that the risks of wasted effort are so great with small releases, and conversely that the increase of information obtained with larger releases is so marked, that the small releases should be avoided. The lower limit certainly should not be less than 40 and probably should be set at 50 or even 70.

Table 8

CLASSIFICATION OF OPERATIONS

Figures in brackets are numbers estimated as described in text

(i) By ecological character of tagging location as in Table 3

Operations In	No. of Operations	No. of Operations Scoring Better than Average		
		For p	For t	For B
Sea-water	3	3 (1.2)	2 (1.0)	2 (1.0)
Estuary marine zone	29	9 (12.1)	11 (10.0)	10 (10.0)
Brackish water	7	4 (2.9)	3 (2.4)	3 (2.4)
Fresh water	2	1 (0.8)	0 (0.7)	1 (0.7)
Total	41	17	16	16

(ii) By behavioural characteristic of the fish as in Table 4

Fish	No. of Operations	No. of Operations Scoring Better than Average		
		For p	For t	For B
Awaiting migration	12	6 (5.0)	3 (4.7)	4 (4.7)
Migrating	2	2 (0.8)	1 (0.8)	1 (0.8)
Dispersed	27	9 (11.2)	12 (10.5)	11 (10.5)
Total	41	17	16	16

(iii) By numbers released

Numbers Released	No. of Operations	No. of Operations Scoring Better than Average		
		For p	For t	For B
Less than 40	16	7 (6.6)	3 (6.2)	4 (6.2)
More than 40	25	10 (10.4)	13 (9.8)	12 (9.8)
Total	41	17	16	16

With these results in mind the results of the first two parts of Table 8 may be reconsidered and it is found that the operations of the brackish water category (part (i)), include five (of seven) which were less than 40 at release, and although this set includes two with nil results, the score for this category is on all counts slightly better than estimated. Although the figures are small this might mean that releases in brackish water, under circumstances similar to those of the operations recorded here, are likely to be successful since they seem to have overcome the disability of small releases. No other modification of the conclusions from these tables appears to be required.

In Table 8 the various indices have generally all supported the conclusions reached, except in part (iii) where p gives a result differing from those of t and B; B then serves to determine the issue. In Table 7 only six operations score better than average on all counts; 18 other operations score better than average for one or other of the p and t indices, and for these, obviously, a compound index like the one used here is the only clear way of making a judgment.

There was evidence that the cooperation from fishermen was not as good as could have been wished. Firstly, the greater success of the Port Hacking operations (particularly Nos. 51-55) as compared with those of other localities can be ascribed to the continuity of the laboratory operations and to more successful publicity, which kept the matter constantly before the fishermen. During much of the period of operations experimental netting was conducted in the Port and many of the recoveries were made by the Division's own nets; the laboratory workers were constantly searching for the tags and the fishermen who did the netting were keenly interested. Hence it is felt that, other things being equal, the success of recovery in any experiment was probably in proportion to the interest of the fishermen. It is possible, though improbable, that the intensity of fishing in Port Hacking, as measured by the relation of frequency of fishing, amount of gear, or magnitude of catch, to population, was greater than elsewhere. Secondly, there were reports from other localities of tags having been recovered and not sent to the laboratory. In consequence it is clear that future operations should be conducted within limits imposed by the ability to maintain interest among fishermen and some kind of supervision to ensure the return of recoveries.

It is of interest, and perhaps significance, in relation to this problem, that the majority of recoveries were made "at the net", and relatively few at markets or at other points along the distribution line where discovery might be presumed more likely.

V. RESULTS

The operations were carried out for the general purpose of studying the biology of the mullet with particular reference to three distinct aspects, viz. movements, growth rate, and mortalities. In analysing the results it is necessary to deal with each aspect separately. This is somewhat artificial because factors which determined movements also influenced mortalities.

(a) *Movements*

The results must be considered first for information on the direction, time, and extent of the movements. This information may be regarded as the primary result of the experiments, and may be examined *per se;* however, if examined in relation to the general biology of the fish it suggests certain conclusions, firstly on the connection between feeding and spawning habits and the selection of the environment by the fish, and secondly on the proportion of the population involved each year in these movements. It will be appreciated, following the information already published on this species (Kesteven 1942), that this work is striking close to the heart of the problem of the biology of the species, and that its results should suggest clearly the direction in which further work should proceed.

(i) *Direction of Movement.*—The results reported previously (Kesteven 1942) indicated that movement, where shown, was consistently northwards. In Table 9 these results are included with those of the present investigation.

TABLE 9

MOVEMENT OF TAGGED FISH

Recovery	Recoveries Made to		
	July 1941*	February 1946	Total
At point of release	24	133	157
North of point of release	42	19	61
South of point of release	—	1	1
No information	2	3	5
Total	68	156	224

* To recovery 68, as reported previously (Kesteven 1942).

The only valid instance of a recovery made south of the point of release (No. 122) was one by laboratory personnel; the fish was immediately released again. There seemed to be very little doubt in the matter. One other tag (No. 112) was returned by a Port Hacking schoolboy, with the information that the fish to which it had been attached had been caught at a point about 120 miles south of its point of release. Since the time given for recapture allowed only 24 hr for the journey of 120 miles, and in view of other circumstances of the report, it was held that this must constitute a "no information" case.

The one valid recovery (No. 122) south of the point of release does not affect the principal result, namely that the aggregate effect of movement is a northward transfer. Even so it would be unwise to suggest on these results that the fish only rarely moved southwards. The evidence on the general biology of this species (Kesteven 1942) requires that at some time there must be some southward movement; the schools of fish observed migrating northwards in autumn are so great and numerous that at first one would suspect that the relative proportions of non-moving (69.7 per cent.) and moving (27.7 per cent.) fish indicated in Table 9—even allowing for recaptures made before an opportunity of moving occurred—could hardly represent truly the proportion of the population involved in these movements. This question of the proportion involved in movements is discussed further below, but it is necessary to point out here that a deficiency still remains in our evidence on the question of direction of movement. In the author's view the results to date suggest the following hypothesis:

(1) *Adult fish which move from their native water* (i.e. those in which they achieve maturity) *move northwards to begin with and at some time, either in the same migration or subsequently, may move southwards, but probably not south of the point from which they commenced their migrations; moreover, later movements north are possible also.*

Conceivably the form of the present results, with few "south" recoveries, is due in part to the fact that a large proportion of the operations took place at Port Hacking, which lies somewhat to the south of the major commercial operations upon this species. Probably the likelihood of recapture south of Port Hacking of fish released there would be a great deal less (however consistent their movement) than that of recapturing fish released, say, in Moreton Bay, which if they moved south would move into the area of intense mullet fishing of northern New South Wales. This possibility can be assessed only by further work.

A further point which should be noted here is the relation of the movements to size, sexual condition of the fish, and so forth; the operation of these factors would not, it is thought, invalidate the above observations, but further consideration will be given to them below. However, since most of the releases were of immature fish, it might be supposed that the fish were released in their native waters. Since available evidence (Kesteven 1942) indicates that the dominant northerly movement is made chiefly after maturity, even allowing for the possibility of partial southward movement by mature fish, the sum effect unless otherwise compensated is a northward movement, which would mean depopulation of the southern grounds. Since such depopulation obviously does not occur, the only conclusion possible is that a southerly transfer of stock occurs among the immature groups—either larval, post-larval, or young fish of I +. If this argument is accepted it requires the following corollary to the above hypothesis:

(1*a*) *If there is any southward movement it must be within the first* 2 *yr of life, or certainly before maturity is reached.*

(ii) *Extent and Time of Movement.*—Table 10 shows an analysis of movements in terms of distance travelled and time spent. It will be seen that movements in excess of 400 miles were recorded. Very approximately, the longer a fish was free the greater was the distance travelled, but there is no simple positive association of duration of freedom with extent of movement. One fish travelled 460 miles in 42 days and another was recaptured only 40 miles from its point of release 656 days after release. The mean travel for each successive 100 days, however, is indicative of greater travel for greater freedom. The rates of travel are of course only minimum rates, since the fish may have accomplished their journey in a very small fraction of the time of freedom. Moreover, there is the possibility referred to earlier that the fish may have been moving back and forth, with a residual effect placing them north of their point of release; if this occurred the real rates of travel would of course be considerably greater than those shown in Table 10. It is perhaps necessary to add that there is no positive evidence, apart from recovery 122, that along-the-coast movement by fish such as those tagged is not entirely northward; but the possibility of southward as well as northward movement must be retained in our hypothesis.

TABLE 10

ANALYSIS OF MOVEMENTS IN TERMS OF DISTANCE TRAVELLED AND TIME SPENT

Recovery Number	Days of Freedom	Distance from Point of Release (miles)		Rate (miles per day)†
		Individuals	Average*	
4	18	50		3.11
3	24	50		2.08
2	32	60	143	1.88
66	42	140		3.33
155	42	460		10.95
68	53	100		1.92
23-53	125	40		0.30
174	148	45		0.30
10	161	450	157	2.78
158	183	210		1.15
8	228	250		1.10
202	267	190		0.71
85	261	50	129	0.19
89	298	25		0.08
21-22	311	40		0.12
92	343	25		0.07
94	375	25	40	0.07
67	377	70		0.18
13	409	50		0.12
91	414	250		0.60
95	418	350	191	0.83
93	421	300		0.71
203	441	6		0.00
121	656	40	40	0.06
122	730	70		0.10
223	741	10		0.01
157	774	63	101	0.08
153	791	260		0.33
156	879	350	350	0.40
159	934	420	420	0.45
224	1012	375	375	0.37
Average	257		98	0.38

* Averages calculated for fish in 100-day-interval groups.

† Represents minimal rate of travel since the distances in the preceding columns are only distances between release and recovery points.

These results are extremely difficult to interpret, as will be seen from the following case. From experiments 20 and 21 at Ballina on the Richmond River in May 1939, four recoveries were made almost within a month, three a short distance north, the other in the locality of release. These fish were fully ripe and it is fairly clear that, passing out of the Richmond River, they went immediately north. About 7 months later another fish from this experiment was recovered at Tewantin about 250 miles north; the questions then arise: did this fish make the longer journey at once, and would the others caught have done so if they had not been caught, or was the longer journey the result of a subsequent migration? Twelve months after the experiment another fish was captured at about the same locality as the first three. This fish could have been in company with others from which the fourth of those taken in the first month could have been captured, or it could have moved with either or both of the earlier groups whose later movements brought them back to this point. These results indicate either:

(*a*) Fragmentation of the schools and completely independent movement, slower and shorter in some than others, or

(*b*) Very wide oscillatory movements in the course of which capture could be made, but the extent and nature of the intervening movements could not be assessed. No decision could be made between these possibilities.

No additional information on the time at which the mullet travel is available from these records. It is impossible to tell from the recoveries when the movement actually took place, and it will require a more closely patterned scheme of operations before such evidence could be obtained. Of course it must be recognized that such a line of inquiry will relate to the precise time of movement of the stock of each river system; that is, the general time of movement of mullet is well known, but there is no way yet of determining accurately when the fish of a particular river system have embarked upon their migration or how the movements of the stock of each water are related in time to one another; or of identifying the origin of any travelling group of fish.

Despite the deficiencies of the present results, the results given in Table 10 suggest the following hypotheses:

(2) *This species is capable of relatively rapid migrations covering long distances and, since the average distances travelled tend to be greater for greater periods of absence, participation in more than one migration could contribute.*

(3) *Such movement could be repeated each successive year thereafter.*

It should be pointed out at this stage that whereas in most other tagging experiments the recoveries made at the locality of release, or within the same season, have generally been excluded from consideration, this has not been done in analysing the results of this work. The problems of mullet behaviour invest some local and early recoveries with a significance which could be quite absent from similar recoveries in other species.

An examination of Appendix I suggests that "absence of movement" might be associated with a shorter duration of freedom than that of the fish which moved. Whilst it is shown in Table 7 that the average number of days of freedom of all recovered fish was approx. 190, it is shown in Table 10 that the average duration of freedom for fish which moved was 257 days, and for fish which did not move 164 days. This result is not as precise as it might be since in effect it includes comparisons of fish from operations on different ages; the comparison should strictly be made between fish from the same operation. Although the data are insufficient to permit extensive comparisons of this type, they are sufficient to confirm the above result and the suggestion that the movements are principally associated with relatively prolonged periods of freedom, or conversely that fish recaptured in the water in which they were released are recovered in relatively short time, possibly before the opportunity to migrate occurs. Of course there are exceptions—not only such instances as the fish (recovery 155) which travelled over 460 miles in 42 days and which was tagged immediately prior to a migration but, of greater significance, instances of fish recaptured in their native waters after periods in excess of 1 yr, including at least one opportunity for travel. These exceptions can be understood in relation to the general biology of the species and will be discussed from that point of view.

(iii) *Proportion of Population Involved in Movements.*—In Table 9 it is shown that 157 (69.7 per cent.) of the recovered fish were taken in the locality where they were released and 62 (27.7 per cent.) in other localities. Of the 157 some were recaptured before they would normally have travelled; that is, they were tagged after the travelling season of one year and recovered before the travelling season of the next. Although it would not be correct to exclude altogether from consideration in this section the fish which were recaptured before having had an opportunity to travel, it will be recognized that such prematurely recaptured fish must be excluded from calculations to determine the proportion of the population migrating each year.

As stated earlier, it is impossible yet to say precisely when the fish of any particular estuary embark upon a migration; at times fishermen observe the fish leaving the river and entering the sea, but they obviously could not say with certainty that such fish represented the whole or any particular proportion of the population of that river system, or whether such fish were commencing their migration from that estuary or had commenced it further south. Consequently it is virtually impossible to say definitely when opportunity to travel occurred, and therefore difficult to classify the non-travelled returns as having been taken before or after opportunity to travel; however, this classification has been made roughly on the basis of information on the times at which the travelling mullet appeared at each point along the coast. It is necessary to keep in mind the account of the *en echelon* character of the mullet migration on this coast, given by Kesteven (1942, pp. 12, 59-60).

TABLE 11

CLASSIFICATION OF RETURNS ACCORDING TO WHETHER FISH HAVE TRAVELLED OR HAD OPPORTUNITY TO TRAVEL

The numbers are recovery numbers

Recovered at localities other than where released

2, 3, 4, 8, 10, 13, 21, 22,
23, 24, 25, 26, 27, 28, 29, 30,
31, 32, 33, 34, 35, 36, 37, 38,
39, 40, 41, 42, 43, 44, 45, 46,
47, 48, 49, 50, 51, 52, 53, 66,
67, 68, 89, 91, 92, 93, 94, 95,
121, 122, 153, 155, 156, 157, 158, 159,
174, 202, 203, 221, 223, 224

Recovered in the same locality as released

Taken between release and next travelling season

5, 6, 7, 12, 15, 57, 58, 59,
61, 62, 63, 71, 72, 86, 97, 98,
99, 100, 101, 102, 103, 104, 105, 106,
107, 108, 109, 110, 113, 114, 115, 116,
117, 118, 119, 120, 123, 124, 125, 126,
127, 128, 129, 130, 131, 132, 133, 134,
135, 136, 137, 138, 139, 140, 141, 142,
143, 144, 145, 146, 147, 148, 149, 150,
151, 152, 154, 176, 189, 190, 191, 193,
194, 195, 196, 197, 198, 199, 200, 201

Taken after next travelling season

1, 14, 16, 17, 18, 19, 20, 54,
55, 56, 60, 64, 65, 70, 74, 75,
76, 77, 78, 79, 80, 81, 82, 83,
84, 85, 87, 90, 96, 111, 160, 161,
162, 163, 164, 165, 166, 167, 168, 169,
170, 171, 172, 173, 175, 177, 178, 179,
180, 181, 182, 183, 184, 185, 186, 187,
188, 192, 204, 205, 206, 207, 208, 209,
210, 211, 212, 213, 214, 215, 216, 217,
218, 219, 220, 222

In Table 11 the returns are grouped in three categories; it will be seen that of the non-travelled fish only 76 are considered as taken in the waters of release *after* an opportunity to travel had occurred; with the 62 travelled fish the 76 non-travelled fish give a total of 138, which is the proper group for consideration in this matter. Thus 45 per cent. of this group have certainly travelled; it is possible that some of the remainder travelled from their point of release and returned to it, and it is held (hypothesis 1) that this possibility is quite real; if so, then 45 per cent. would be an underestimate of the proportion of stock which travels. On the other hand, a few returns were made after absences of more than 1 yr—that is, embracing two or more normal migrating periods—and such fish might have remained in their home waters during the first year of freedom and travelled in the second, or vice versa; for this reason again the figure 45 per cent. might not represent the proportion of the population moving in each year. (It is to be borne in mind that these results apply only to the groups tagged as described in Section II, and to the tagging times and localities.) At this stage it is impossible to attempt any adjustment of the figure 45 per cent. in accordance with either of the two above possibilities, but it is felt that the evidence indicates that at least half of the mature and maturing (II +) population engages each year in the migration, and conversely that a proportion might refrain from travel.

The above results are presented in Table 12, in summarized and somewhat different form.

TABLE 12

RECOVERIES OF MIGRATING AND NON-MIGRATING FISH CLASSIFIED BY AGE AT RELEASE AND PERIOD OF FREEDOM

Left-hand figures are of fish which have moved, right-hand figures of fish caught in the locality of release. The discrepancies between the totals and those of Table 9 are due to the exclusion of certain fish because scales were not taken or were unreadable

At Release		Period of Freedom (yr)						Totals
Size (cm)	Age	0-½	½-1	1-1½	1½-2	2-2½	2½-3	
15.1-23.0	I+	0,11	1,4	0,1	1,0	1,0		3,16 = 19
23.1-32.0	II+	33,57	3,32	2,4	1,2	1,0	1,0	41,95 = 136
32.1-40.0	III+	7,21	4,12	4,0		1,0		16,33 = 49
40.1-48.0	IV+	2,5	0,1					2,6 = 8
48.1+	V+	1,0						1,0 = 1
Totals		43,94 = 137	8,49 = 57	6,5 = 11	2,2 = 4	3,0 = 3	1,0 = 1	63,150 = 213

This table neglects the important factors of the locality and time of year of release. However, it indicates firstly, the general inadequacy of the results and secondly, that after 1 yr of freedom the majority of the fish (12 of 19) enter upon some migration; and it possibly suggests that, given sufficient time, every fish will migrate, since only two of eight fish free for more than 1½ yr were recovered at the same locality as that in which they were released.

So far reference has been made only to time and place as possibly significant factors, but it is recognized that the age and bionomic status of the fish are probably the basic factors; these factors are partially expressed in age and size but can be understood only in terms of a detailed knowledge of the environment of the fish and of their physiology (gonad condition, feeding behaviour, fatness, etc.). In default of such information it is unwise to press the analysis of these data any further; it is hoped, however, that they might yield further information when other more fully documented returns point the way to a better understanding of the problem.

Reliable evidence from field observations and the reports of fishermen suggest that immature fish make only short migrations and generally return to their native waters. This point requires further investigation, because if it could be established the migrations of mature and immature fish should be considered quite separately; in particular, no comparison of migrated and non-migrated fish should be made involving immature stock. However, there is no evidence on which to attempt such a separation, and although size is a general index of maturity, there is no noticeable size difference between any of the three categories in Table 11. Nevertheless, gonad condition is a further factor which undoubtedly would, if measurable, reduce the total of fish validly identified as non-travelling and increase the proportion of travellers.

Whilst there is considerable evidence that some proportion at least of the mature population remains in the estuaries and lakes at the time of the major autumn migration, this is principally negative evidence. It is conceivable that in all such apparent instances there had been migration and the fish had returned to their native waters. One reason why such fish might abstain from migrating is that they matured 1 or 2 yr later than the general population and deferred migration accordingly; alternatively, there might be a total migration upon first maturity and then migration in alternate years only, or in some other rhythm.

On the results to date it is felt that the following hypothesis is indicated:

(4) *Most mullet migrate upon first achieving maturity; it is possible that they do not all migrate every year thereafter, but probably more than* 50 *per cent. of the mature and maturing population of each year engages in the migrations.*

(iv) *Frequency of Movement by Individual Fish.*—It is stated in hypothesis 3 that each fish can presumably make further journeys in successive years. This hypothesis is based on the greater amount of travel by fish which have more than one opportunity of participating in a migration, as compared with those having only one. This is by no means conclusive but is supported by some further evidence in this work, e.g. the results of operations 20 and 21 discussed above, which should be considered with the result of experiments 39 and 40. From these later experiments (Terranora Creek and Currumbin Creek, May 1941) recoveries were made in the locality of release within 9 months, and then the fish, many of which were I +, must have moved out as hardgut mullet and travelled a short distance north. Within the next 3 months some were taken about 25 miles north and one was taken there 10 months later (1943). In

June 1943 one was taken in the normal travelling season at Cape Moreton still further north. This type of evidence suggests a multiplicity of migrations for each fish.

However, this question must be considered in relation to the whole biology of the species, and the entire range of evidence thereon available from this work. Thus our understanding of the biology of the species is that after spawning the fish re-enter the river systems and make their way to the head waters where they remain for about 6 months, coming down stream again in the following season. This is supported by the tagging operations. Firstly, tagging returns have proved that the fish from the head waters do go to sea (operation 23) and that after going to sea they return to the river systems (e.g. recovery 10). Secondly, the tagging results show the spawning schools to be drawn in part from the middle waters of the river systems. Thirdly, the results show a general participation in these movements.

Whilst no attempt can be made to estimate from the data of these experiments the number of times a mullet may travel to sea and spawn, the weight of evidence indicates that it is at least more than once.

(v) *Duration of Oceanic Sojourn.*—Whilst the tagging results give some rough estimates of speed of travel and suggest that the actual coastal movement is accomplished in a relatively short time (3 wk from Port Hacking to the Queensland border), there are undoubtedly preliminaries and delays which cannot be estimated. However, the "travelling" season lasts only a few weeks at each locality and since, in view of the *en echelon* character of the movement along the coast (see below), the observations at each locality are of the seagoing activity of its stock and stock from south of it, it is concluded that the oceanic sojourn of the mullet cannot occupy more than 4-8 wk.

(vi) *Continuity of Movement along Eastern Australian Coast.*—The most noticeable feature of the biology of this species is the extensive and massive movements of the stocks northwards along the coast during autumn. These movements are observed every year and the fishermen make a practice of waiting with their gear on the headlands and beaches, at the time appropriate for their section of the coast, for the appearance of the schools. The number and the magnitude of the schools vary at each locality from season to season, and there is some variation in their composition.

There has been some controversy as to the origin of these schools, but earlier work (Kesteven 1942) established that they came from the coastal lakes and streams. Consideration of all results to date shows conclusively that the general outline of the biology of this species given in the earlier paper is well founded, and that the schools of fish observed on the coast are formed by the congregation within the lakes, rivers, and estuaries of the fish which have been subject to fishing in those waters during the remainder of the year and during their subsequent movement to sea.

Tables 1-4 show that the various habitats and behavioural types of mullet are all represented in the tagging operations and a summary of these is presented in Table 6. Table 13 shows "travelled" recoveries from each of the seven categories of releases, and although these recoveries are not numerous they are sufficient to show the continuity of these stocks as between habitats.

The outstanding question then is: what relationship is there between the schools observed at various points along the coast?

TABLE 13

MIGRATED FISH CLASSIFIED BY HABITAT AND BEHAVIOURAL PHASE AT RELEASE

Cf. Table 6. The figures are recovery numbers

Habitat	Behavioural Phase		
	Awaiting Migration	Migrating	Dispersed
Sea-water	67	2, 3, 4, 8, 13	
Marine zone of estuary	20-53, 68, 89, 94, 121, 155, 157, 174		91, 93, 95, 153, 156, 158, 159, 202, 204, 220, 221
Brackish water	66		122
Fresh water			9(?), 10

Figure 2 shows the paths of movement (which it must be remembered are residual) of the "travelled" returns; it will be seen that this reveals a continuous interlocking series of movements from Victorian waters north into Queensland waters. It is apparent from this figure and the data from which it was drawn that there is no barrier to the movements of these fish along the coast; but the diagram gives no clue to the details of movements in each year. The movements could be relatively restricted, but it is equally possible that there are very extensive and complex movements of which only the simplest features are revealed by this work. However, present information on the movements is generally as follows:

> The factors determining the initiation of migration from any particular water and the extent of migration by the stock of each water are as yet unknown;
>
> In any season the entire stock of the coast or of a large stretch of it may migrate more or less simultaneously, but more generally there is an *en echelon* effect as to both the time of commencing migration and the stretch of coast covered;
>
> In general there is a shift north, the fish of one water replacing those of another north of it;
>
> In the course of such movement, however, the various populations may remain completely separate, or there may be intermingling;

It is possible but unlikely that the population of a particular water might refrain completely from migration;

The population from one water might move into, out of, or beyond waters occupied by another (before, when, or after that population moves), and travel to a point short of, the same as, or beyond that reached by the other, initially more northern, population. It is considered that the results from tagging operations, with the evidence of fishermen's reports and of catches taken, indicate that such a complicated pattern of northward movement, replacement, and intermingling takes place on this coast.

The recoveries of tags from fish which travelled are grouped in Table 13. Recoveries 8 and 10 were commented upon previously (Kesteven 1942), the one as showing the extent to which "river" fish migrate and the other as showing the distance to which fish from New South Wales penetrate into Queensland waters. Recoveries 66, 67, and 68, also commented on in the earlier paper, showed something of the continuity of the along-the-coast movement of this stock; this evidence was supplemented by recoveries 91-94, 121, 153, 155-159, 174, 202, and 224. Of these, recoveries 153 and 156 are particularly interesting since they indicate that the catches taken in the Clarence River system (including all its lakes etc.) include some fish from southern waters; no useful conjecture may be made at this stage as to how far this system is dependent upon southern waters for recruits to its fishable stock, but it will be appreciated that the question is of significance, particularly in view of the great importance of the Clarence River as a source of mullet. Interest attaches both to the point of release of these fish and to the point of recapture, not only because of the distance between the two points but also because of the ecological and economic implications. The predominance of Port Hacking as a point of release for these recoveries is due of course to its predominance in the tagging operations, but this is a relatively small water system probably with proportionately small living space for mullet, though it clearly makes contribution to the mullet catch in other waters. It is reasonably plain that the exchanges between the various water systems are substantial and consistent.

(*b*) *Growth Rate*

Appendix I gives information on the length of each fish at release and at recapture. The difference between these lengths, which should represent the amount the fish grew during its freedom, is also recorded together with the number of days of freedom. Scales were taken from the fish at release in most operations and at many recoveries; the reading of the pairs of scales gives useful data on the problem of scale reading and on the growth of the species. Before presenting these results, it is necessary to discuss some questions concerning the technique of scale reading.

The estimates of growth given in Appendix I include negative, nil, and positive figures of varying significance. It is difficult to decide on the reliance to be placed on some of the figures. Every precaution was taken to ensure accuracy in measuring and recording at release, and every effort made to obtain possession of the fish at recapture rather than rely upon reports of measurement, and the majority of the estimates of growth appear acceptable, but certain of the results nevertheless appear quite unacceptable. Thus recoveries 17 and 18 indicate shrinkages of 9.0 and 6.5 cm respectively, and since as far as we know shrinkage of this degree, even with extreme starvation, is impossible, it must be assumed that inaccuracy in measuring or recording occurred at release or recapture.

Although measurements are always made by the official measurers to the nearest millimetre it is not held that a particular result in measuring a particular fish could be exactly reproduced even on the same occasion; variations of a few millimetres can arise from failure to place the snout of the fish precisely at the head-piece of the measuring board or from differences in flexure of the fish; variations of centimetres are possible from careless reading; and recording errors could account for a wide range of variation. Unfortunately such errors are by no means systematic or easily distinguished, and it has been necessary to employ various means in their detection. For instance, recovery 218 was recorded as having a length at recovery of 30.7 cm, and at release of 32.7 cm; this might be regarded as a small error of reading (the possibility of a shrinkage of this amount being disregarded), but when the scales were examined it was found that the fish was I + at release whereas it was II + at recapture. The scales at recapture showed breaks at 15.8 and 25.0 cm and if it is assumed that the break found in the scales taken at release should mark l_1 at the same length as shown in the scales taken at recapture, i.e. at about 15.8 cm, the length of the fish at release should then be taken as 22.7 cm (see below); thus what appeared to be a small negative error of measurement at recapture was shown to have been in all probability a quite large positive one (10 cm) of reading or recording at release. Again recovery 183, which at first sight seems to be a similar case of slight under-measurement at recapture, is thought, after reference to the scales, to involve a deficiency of 1.4 cm in measurement. It would be reasonable ordinarily to regard a negative value of as much as 5 mm as the result of minor errors in measuring and re-measuring the fish and to take this to mean that no growth had taken place; fallacious assumptions of this kind are avoidable by using the two sets of scales. The foregoing examples show the need for rigorous care in accepting these measurements, and the following rules were adopted in the present work:

(1) Since checks of accuracy are maintained during a release operation measurements at release are taken to be valid, unless there is contrary evidence.

(2) Large shrinkage is regarded as impossible and where reported is taken to indicate a major error of measurement; small shrinkages are regarded as being errors in remeasuring the same length, i.e. as indicating that no growth has taken place.

(3) Small positive estimates (less than 5 mm) of growth are regarded (unless scale or other evidence points to the contrary) as measurement errors and it is assumed that no growth has taken place.

(4) Although considerations of season and locality must be borne in mind, a lapse of time is taken to be presumptive evidence of growth; i.e. if growth is shown and there is any question as to its validity a lapse of time is supporting evidence.

(5) Comparison of scales taken at release and recapture is regarded as a sound means of detecting errors and indicating possible adjustments; increase in scale size by either whole annuli or number of circuli is taken to represent growth, and when one or the other measurement is rejected it is replaced by a value calculated from the relative increase in scale size.

Summary of Principal Experiments

Release operation No. 48, *January* 5, 1943, *Port Hacking*

Recoveries: 23.

Recovery 104: 31.9 to 32.0 cm, 15 days; see also recoveries 106, 107, 108, 114, 115, with no growth.

Recovery 133: 31.2 to 33.0 cm, 93 days, growth 1.8 cm. See also recoveries 138, 143, 144, 146, 158, 160, 163, 173, 178-81, 128-134, at 93-279 days' absence, growth up to 3 cm.

Recovery 205: 30.4 to 36.0 cm, 590 days, growth 5.6 cm.

Recovery 219: 28.4 to 37.2 cm, 619 days, growth 8.8 cm.

From this operation the six recoveries in the first 2 months showed no growth; 15 recoveries within 9 months of release showed only minor growth. Unfortunately no further recoveries were effected until 10 months later (21 months after release); two recoveries then made both showed substantial growth, equal, however, to only 1 yr of growth. These results suggest that little growth takes place between January and October, leaving October to the end of December as the principal growing season.

Release operations Nos. 49 *and* 50, *February* 3 *and* 4, 1943, *Port Hacking*

Recoveries: 21.

Recovery 112: 32.1 to 32.1 cm, 1 day. See also 113, 116-120, 123, 124, 126, 129-132, 139, 142, 150, 161, 162, 172, 177. Mostly nil and negligible growth, but up to about 2 cm at 64 days and more.

None of these recoveries showed much growth, the greatest period of freedom being 249 days, to the beginning of October. This confirmed the results from operation 48.

Release operation No. 51, *March* 19, 1943, *Port Hacking*

Recoveries: 12.

Recovery 125: 30.6 to 30.6 cm, 10 days. See also 149, 151, 165-7, 175, 182, 191, with no growth up to 206 days' absence; measurements to 165 are regarded on scale evidence as inaccurate.

Recovery 203: 35.9 to 40.5 cm, 441 days, growth 4.6 cm.

Recovery 211: 28.0 to 35.1 cm, 536 days, growth 7.1 cm.

Recovery 223 from this experiment was returned without information. Recovery 165 was recorded as showing growth of 3.6 cm in 179 days, to September, but examination of the scales indicated that very little growth took place, and a measuring error was assumed. Hence the nine recoveries made before and during October showed no growth. Recoveries 203 and 211 showed good growth; 211, which was free for a further 3 months, showed somewhat the greater growth, but this was more likely to have been due to the lesser age and size of the fish when released than to the extra time of freedom; and was not considered evidence for appreciable growth between June and September. In general the results of this operation confirmed that growth in the early half and middle of the year is small or absent.

Release operations Nos. 52 *and* 53, *April* 8 *and* 15, 1943, *Port Hacking*

Recoveries: 25.

Recovery 137: 30.0 to 29.7 cm, 50 days. See also 135, 136, 140, 141, 145, 147, 148, 152, 154, 155, 164, 168-171, 174, 183-188, with no appreciable growth up to 179 days

Recovery 204: 24.6 to 30.0 cm, 485 days, growth 5.4 cm.

Recovery 210: 24.1 to 33.0 cm, 510 days, growth 8.9 cm.

From this operation 23 recoveries were effected to October in the year of release, with absences up to 186 days. No appreciable growth was recorded for any of these fish except No. 170, but the scales showed that the growth of this fish was actually very small. Appreciable growth was shown by the last fish from the operations, Nos. 204 and 210.

Release operations Nos. 39 *and* 40, *May* 15 *and* 16, 1941, *Terranora Creek and Currumbin Creek, Tweed River*

Recoveries: 19.

Recovery 72: 23.0 to 22.3 cm, 29 days, apparent shrinkage counted as nil growth. See also 72, 74-76, 79.

Recovery 63: 25.6 to 28.0 cm, 19 days, growth 2.4 cm. See also 77, 80, 81.

Recovery 83: 23.3 to 29.2 cm, 206 days, growth 5.9 cm. See also 87, 88, 89.

Recovery 90: 23.2 to 30.5 cm, 312 days, growth 7.3 cm. See also 92, 94, 96, 121.

Recovery 157: no information.

This operation took place a considerable distance north of those referred to so far; it would not be surprising therefore if its results should differ from those of the other operations. Growth is shown to have commenced in October-November and to be well established by December. In the above list the recoveries are placed in four groups, with no growth, small growth, mean growth about 5.0 cm, and mean growth about 8.0 cm respectively; the 8-cm group was absent longer than the 5-cm, but the differences of growth and absence are hardly quantitatively associated. These results suggest that the growing period is possibly longer in this region than further south.

Release operation No. 46, *June* 25, 1942, *Port Hacking*

Recoveries: 9.

Recovery 97: 31.6 to 31.9 cm, 126 days. See also 98-100, with growth under 1 cm.

Recovery 102: 31.0 to 32.2 cm, 189 days, growth 1.2 cm. See also 103.

Recovery 105: 27.1 to 29.5 cm, 223 days, growth 2.4 cm. See also 109.

Recovery 127: 25.0 to 29.5 cm, 287 days, growth 4.5 cm.

Growth was small, possibly nil, in the fish recovered in October and early December, but was progressively greater in fish recovered in late December, February, and April.

Release operation No. 54, *September* 14, 1943, *Port Hacking*

Recoveries: 11.

Recovery 176: 30.3 to 30.3 cm, 27 days. See also 189, 190, 193.

Recovery 206: 29.3 to 33.0 cm, 338 days, growth 3.7 cm. See also 212, 215, 217, 218, 219.

Recovery 224: 31.8 to 41.3 cm, 1012 days, growth 9.5 cm.

Three recoveries in October showed no growth. Recoveries in August and September 1944 showed the amounts of growth to be expected after an absence of approx. 1 yr. Recovery 224 showed much greater growth, appropriate to longer freedom, but unfortunately no scales were taken from this fish at recapture.

Release operation No. 55, *October* 11, 1943, *Port Hacking*

Recoveries: 9.

Recovery 200: 30.2 to 33.2 cm, 120 days, growth 3.0 cm. See also 202, 207, 209, 213, 214, 220, 221, 222.

The first recovery from this operation was in February 1944; this showed appreciable growth. Recoveries were made in July, August, September, and November 1924, and February 1945, and all showed appreciable growth; the last recovery (No. 222) showed the greatest growth and the scale shows two "breaks".

Other Operations.—No. 31, February 24, 1941, Port Hacking: Two recoveries; No. 82, taken in November, showed appreciable growth, but greatly exceeded by that of No. 91, taken in April.

Nos. 42 and 43, May 1941, Port Hacking: Two recoveries in January and November 1942 showed good growth.

No. 47, October 1941, Port Hacking: Two recoveries made in December 1941 and February 1942 after only short absences showed no growth.

No. 41, December 1941, Port Hacking: One recovery in February 1942 showed small growth.

No. 30, January 1942, Lake Illawarra: Five recoveries; the first two in June showed moderate growth, the other three considerable growth, appropriate to the absences.

Attention should be drawn to the fact that the initial recoveries of any operation generally showed no growth even if made during or after the growing period. Thus the early recoveries from operations 48, 49, 50, and 51 showed no growth although the fish concerned were free during the first quarter of the year, which as other results indicate probably covers at least part of the growing season. This suggests that possibly the tagging operation exercises a deterrent effect on the growth of the fish, but there is no evidence as to the possible magnitude of this effect.

(i) *Annual Growth.*—The foregoing results substantially confirm the statement made (Kesteven 1942) on the principal features of the growth of this species. At least 44 of the recoveries showed appreciable growth and the amounts shown correspond roughly to what might have been predicted for such periods of absence on the basis of the previous results. The earlier results, however, did not permit of a partitioning of the calendar year into growing and non-growing periods, without which no definite prediction could have been made as to the growth for portion of a year.

The present results are plotted in Figure 4 with the earlier estimate of amount of growth per year drawn as heavy lines.

The biological year was taken arbitrarily to commence at the beginning of May, but even if this should prove to be too early or too late there would be no need to change the slope of the line. This is shown in Figure 5 in which the line *ABC* represents the earlier results on the growth of this species; the curves A_1b' and B_1c' conform more closely with what we now know. If a point on AA_1, or on the preceding segment $a'A$, is joined to a second point, on BB_1 or on $b'B$, so that the horizontal distance between perpendiculars through these points represents an interval of 1 yr, the line so drawn will be parallel to *AB*, and many such lines could be drawn. All such lines could accurately represent the growth of the fish between comparable points in two successive biological years. However, if points along the curves A_1b' and B_1c' at equal time intervals are connected, there will be found a transition of slope; *AB* has a slope of

36° 12′ and *BC* one of 33° 42′, and the intermediate lines are at slopes of 37° 1′, 36° 24′, 35° 18′, 34° 51′, and 34° 32′. (These values are of course fortuitously determined by the way in which the curves *A′b′* and *B′c′* have been drawn.) These differences are not very great but they account for some of the differences among the lines in Figure 4. On the other hand, the lines in Figure 4, representing the growth of tagged fish during their period of absence, would also be expected to depart from parallelism with the heavy lines for the following causes:

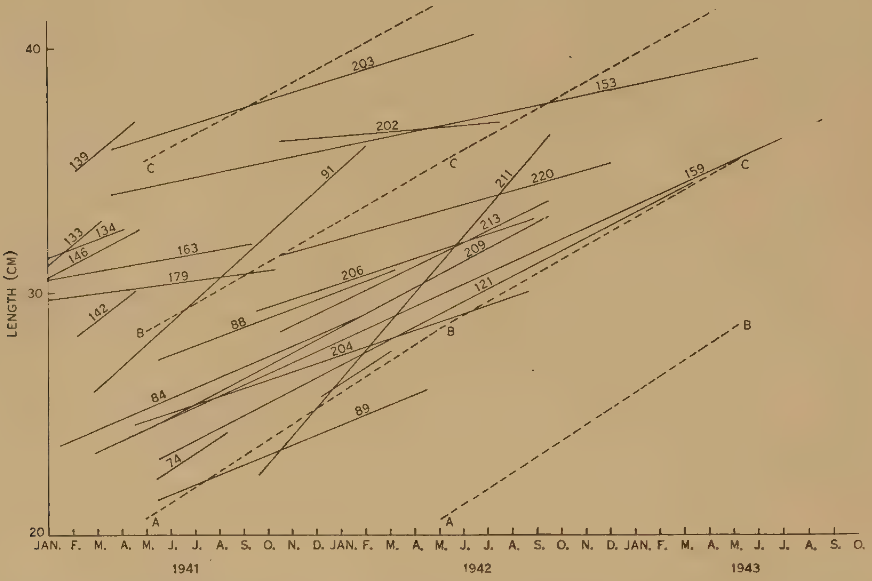


Fig. 4.—Growth of tagged fish during period of absence. Each line represents the growth of a tagged fish between release and recapture. The numbers of these lines refer to the tag recovery numbers (Appendix I). The heavy lines marked *A*, *B*, and *C* represent the average annual growth of this species.

(1) Individual variation from average growth represented by the heavy lines;

(2) Unsatisfactory record; i.e. in only a few cases is the period of absence exactly 1 yr and where it is not, unless the period of absence bears the same ratio to the whole year as the amount of growth does to the average amount of growth for such an age-group, there would be a departure from parallelism. In terms of portions of the year this problem may be described as follows: the slope of the line will be lower than that of the heavy line where the period of absence is greater than 1 yr and includes only one growing period, or where the amount of growing time included in the absence is a smaller proportion of the period of absence than is the amount of non-growing time; the slope will be steeper where the latter situation is reversed.

In Figure 4 many of the individual growth lines are roughly parallel to the heavy lines. Thus the recoveries made before March 1942 from the release of May 15, 1941 (No. 39) are roughly parallel, but the growth lines of later recoveries up to 6 months later are not so steep, which agrees with the latter situation in (2) above. Certain of the recoveries made from the release of January 5, 1941 (No. 48) have growth lines less steep than the heavy lines; some of these are due to each of the above. Closer examination of these lines must be deferred until the evidence on the limits of the growing period is examined. It may be stated at this point, however, that the evidence from this work in general confirms the rate of annual increase in this species shown in the earlier investigations, namely, an increase of *c.* 9 cm in the third year and *c.* 8 cm in the fourth year.

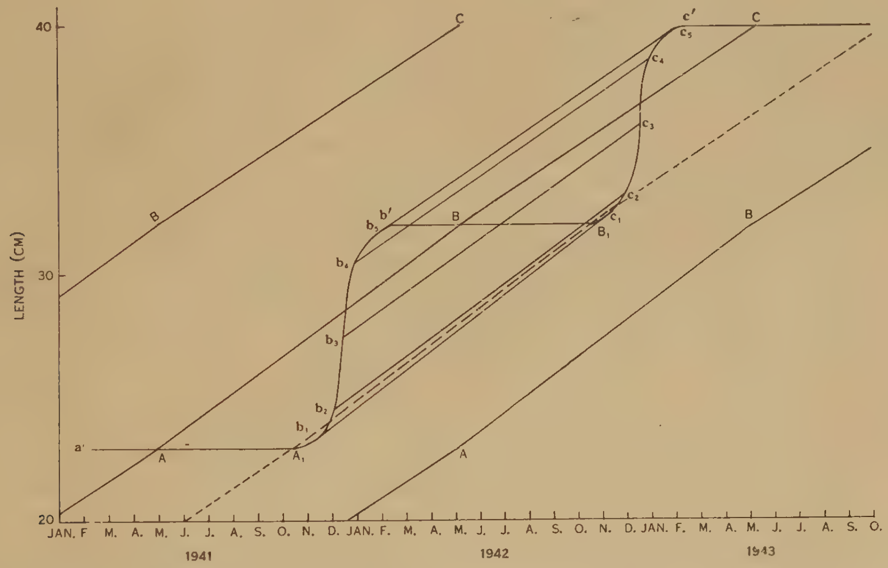

40
30
20
LENGTH (CM)
C
c'
C
c5
c4
c3
c2
c1
B1
B
b'
b5
B
b4
b3
b2
b1
a'
A
A1
A
B
JAN. F M. A. M. J. J. A. S. O. N. D. JAN. F. M. A. M. J. J. A. S. O. N. D. JAN. F. M. A. M. J. J. A. S. O.
1941
1942
1943

Fig. 5.—Diagrammatic representation of growth curves. The heavy lines marked *A*, *B*, and *C* represent the average annual growth of this species. $AA_1b_1b_2b_3b_4b_5b'BB_1c_1c_2c_3c_4c_5c'$ represents the seasonal differentiated growth as shown in this work. The lines A_1B_1, b_2c_2, b_3c_3, b_4c_4, b_5c_5 show result of connecting comparable points on the seasonal differentiated curve.

(ii) *Period of Growth.*—These results demonstrate that the growing period in this species is somewhat limited, although they are too meagre to show precisely either its calendar limits or variability. The recoveries from operations 48, 51-3, 39, 40, 46, and 54 indicate that growth commences mainly after October and at most is commenced in a small way in October. Since operations 48-51 took place in the first quarter of the year and many of the recoveries showed no growth, it might be concluded that this also is part of the non-growing period, limiting the growing period to the last quarter of the year. However, recoveries from operations 31, 46, and 55 indicate that appreciable growth does take place in the first quarter, and the absence of growth in the early recoveries from operations very early in the year perhaps shows the deterrent effect of tagging mentioned earlier. The limits of the growing period would appear to be October to March, with the principal growth occurring in November to February. It is to be noted that this result properly applies only to Port Hacking, from which the most important returns were obtained. Doubtless both the limits and the length of this period vary from point to point on the coast.

(iii) *Scale Reading.*—Scales collected at release and at recapture are available from 78 recoveries. Some of the measurements at release and recapture suggest a reduction in the length of the fish during its absence, but arguments are advanced above for believing that such apparent reductions arise from faulty measuring or recording, and for effecting corrections or rejections. The justification for the latter procedure is that, if it could be established that there was a structural identity between the scales at release and at recapture, then corresponding dimensions on the respective scales would represent similar lengths; if one or other measurement of length could be accepted, then the intermediate lengths calculated on the scales taken with this length could be applied to the corresponding dimensions on the scales taken with the other measurements. Some examples of the application of this principle are given above.

Comparison may be made between scales on the basis of:

(1) The size of the scale as measured along any axis;

(2) The numerable structural features, i.e. the circuli and the annuli. The annuli have been shown to relate to the age and the size of the fish, and this comparison is therefore related to scale size; there are grounds for believing that a similar situation exists for the circuli, and this is discussed further below.

It was shown (Kesteven 1942) that there was some variation in the size of scales from each fish. A comparison between fish on the basis of size is completely valid therefore only when the scales are taken from identical points on the fish; in the present work, where the scales being compared were from the one fish, this condition could not be satisfied. The increments of scale size from release to recapture, plotted against corresponding increments of fish size, revealed an approximate general relationship similar to that in a graph of scale size against fish size for this species. However, the scatter was such as to render the graph of little value. The scatter arose from taking the scales from different points on the fish, from individual differences in average scale size of different fish, and from errors of measurement. The present data are unfortunately inadequate for any statistical isolation of one or more of these groups, but it is possible to approach the matter from a different angle.

As stated above, the number of annuli can validly be related to the age and the size of fish, although there is of course considerable variation in the size of fish at each age. In 23 of the instances in which scales were obtained both at release and recapture new breaks are shown in the scales taken at recapture. Some of the remainder show increases in scale size accompanying small amounts of growth in the fish. None of the latter group (those showing no new break) was free more than 1 yr; on the other hand a few of the former group were free for more than 1 yr and show structural features identical with those found in the scales taken at release (Plate 2); although it has been known as a feature of this species that all the scales of individual fish will reveal the same structural features, the present evidence not only confirms this but also strengthens belief in the essential permanence of the scales and of the record they carry. This point was discussed by Van Oosten (1929).

Although it was previously held that no reliable count of circuli could be obtained in this species, it is now thought that this belief might not be correct. There is indeed some variation in the width of the individual circuli and counting the circuli is at times made difficult by opacity; moreover the circuli are numerous and sometimes considerably fragmented. However, later work has shown that the application of arbitrary rules as to the axes along which circuli should be counted, and as to the identification of the circuli, makes it possible to get results of value. This question is being investigated further, and the present indications are that the number of the circuli is fairly closely related to both the size of the scale and the size of the fish, and that the mean width of the circuli increases with age and with scale size. These results mean that, subject to errors, circuli counts may be used to indicate the size of fish, and more particularly that an examination of the number of circuli shown on scales taken at release and at recapture will serve to indicate whether growth has taken place.

Application of the foregoing principles to the reading of scales from recovered fish referred to above gives the following summarized results:

From operation 48, January 1941, the first scales recovered showed neither growth nor break. Recoveries 205 and 219 showed breaks occurring after some growth had taken place (Table 14).

From operations 49-50, February 1941, all recoveries were made before November, with little or no growth and no break.

From operation 51, March 1941, the situation was as for operation 48, recovery 210 showing a break which, however, was formed before further growth took place.

From operations 52 and 53, April 1941, as for operation 51; recoveries 204 and 209 showed a break.

From operations 38 and 39, May 1941, recovery 83, taken in December, showed a new break before new growth; there was a similar appearance in recoveries 96 and 121 taken in September 1942 and March 1943 respectively, but in 96 only one new break was shown whereas two were found in 121. This supports the view that the break is formed in the portion of the year when growth takes place.

TABLE 14

GROWTH CALCULATIONS FROM SCALE READINGS IN FISH WHERE APPRECIABLE GROWTH WAS RECORDED

Recovery No.	Freedom (days)	At Release		At Recovery						Growth During Absence (cm)		
		Age	L.C.F.* (cm)	Age	Intermediate Lengths (cm)				L.C.F.* (cm)	Before Break†	After Break	
					l_1	l_2	l_3	l_4			1st	2nd
83	206	I+	23.3	II+	10.0	22.9			29.2	—0.4	7.2	
86	86	I+	25.7	II+	14.0	25.0			27.6	—0.7	2.6	
96	477	II+	25.3	III+	10.0	17.6	25.2		30.5	—1.7	5.2	
102	189	II+	31.0	III+	10.0	20.0	30.0		32.2	—1.0	2.2	
103	189	II+	27.1	III+	10.8	18.8	27.6		28.1	0.5	0.5	
111	231	I+	31.4	II+		21.5	30.0		33.7	—1.4	3.7	
121	656	I+	23.2	III+	10.8	23.6	32.5		34.4	0.4	8.9	1.9
156	879	I+	24.1	III+	16.5	30.0	40.0		43.8	5.9	10.0	3.8
204	485	I+	24.6	II+	18.5	24.5			30.0	—0.1	5.5	
205	590	II+	30.4	III+	13.0	27.0	33.5		36.0	3.1	2.5	
206	338	II+	29.3	III+	13.5	21.0	29.8		33.0	0.5	3.2	
207	311	II+	34.0	III+	11.0	25.2	33.5		37.0	—0.5	3.5	
208	345	III+	32.9	IV+	9.0	18.7	26.5	32.3	36.5	—0.6	4.2	
209	324	III+	31.8	IV+	10.0	19.5	26.2	32.0	37.0	—0.2	5.0	
210	510	I+	24.1	II+	13.0	23.8			33.0	0.3	7.2	
211	536	II+	28.0	III+	9.0	17.5	28.4		35.1	0.4	6.7	
212	357	II+	22.5	IV+	11.0	17.0	24.0	31.5	36.4	1.5	7.5	4.9
213	330	I+	30.4	II+	17.0	29.5			36.0	—0.9	6.5	
214	330	I+	28.4	II+	17.0	27.0			33.7	—1.4	6.7	
216	305	II+	21.4	II+	11.0	21.0			29.1	—0.4	8.1	
217	367	III+	32.7	IV+	11.0	17.0	26.0	31.5	36.1	—1.2	4.6	
218	367	I+	22.7	II+	15.5	25.2			30.7	—1.4	5.5	
219	619	II+	28.4	III+	14.5	24.5	33.0		37.2	4.6	4.2	
220	343	II+	31.2	III+	15.0	22.0	32.0		35.0	—0.8	3.0	
222	493	II+	31.5	III+	15.5	28.0	36.0		38.2	4.5	2.2	

* Length from snout to caudal fork. † Before the break first formed after release.

From operation 46, June 1941, recovery 99 taken in early December 1941 showed no new break, whereas recoveries 102 and 103 showed new breaks preceding new growth.

From operation 54, September 1941, the recoveries taken before and in October 1941 showed no break, but recoveries 206, 215, 217, and 218, which were taken after the growing period as established in this work, each showed a new break preceding new growth.

From operation 55, October 1941, recoveries 207, 209, 213, 214, 220, 221, and 223 showed results similar to the late recoveries in operation 54.

From the other operations listed here, recoveries 101 and 58 conformed with the above. Recovery 156 suggests that the break is formed somewhere about December and that growth takes place thereafter.

The instances important for this section, those in which appreciable growth was recorded and a new break revealed in the scales, are listed in Table 14 together with calculated intermediate lengths. Although the latter are calculated from the scales taken at recovery, the corresponding lengths from the scales taken at release were also calculated.

From Table 14, and from the foregoing summary, it is reasonably established that the break is formed in the part of the year when growth takes place. There are only four apparent exceptions to the general rule that the break was formed before new growth was recorded on the scale. In three of these the fish were released in January, within the growing period; this might suggest that the fish continued to grow during the remainder of the growing season in which they were released, ceased growth for several months, formed a new break, and then resumed growth until their recapture. This would be a reasonable hypothesis were it not that other recoveries in greater numbers from the same operations do not show new growth before the break. It is of course possible that the hypothesis is valid and that the two sets of results merely represent differential response of the groups of fish to tagging. In any event the evidence on the time of formation of the break is sound and the following hypothesis is proposed:

(5) *There being no growth during the central* 6 *months of the year (about April to October inclusive), some erosion of the scale and its surrounding tissues takes place in this period; at the end of this period growth is resumed by the surrounding tissues which to some extent may have become reoriented to the existing scale. Subsequent accretions to the scale differ from the existing structure because of erosion, because of the alterations in the surrounding tissues and their relations to the scales, and because of the accelerated rate of growth in the late spring.*

(*c*) *Fishing Intensity and Mortality*

The recoveries from each of the 41 tagging operations are given in Table 7. The 221 recoveries (neglecting the three "no-information" returns) from the 3432 fish released represent an overall return of 6.43 per cent. This figure covers a number of operations from which no returns at all were obtained; it is possible, but hardly likely, that the populations to which the fish were released by such operations were subject to no fishing. On the other hand some operations yielded much greater returns, one of them 26.2 per cent. The disabilities of these recovery figures have been discussed above, and there is no doubt that the real recovery proportion is much higher than 6.43 per cent. It is most significant that although a majority (54.7 per cent.) of the releases were made from Port Hacking, the recoveries from these releases represent an even greater proportion—66.6 per cent., despite the fact that the fishing operations in this water were restricted almost completely to the netting carried out for the tagging work. The overall proportion of recoveries from the Port Hacking releases was 7.84 per cent., but returns of 11.0, 26.2, 9.7, and 18.4 per cent. were recorded from individual operations.

Whilst present evidence suggests that a greater proportion than 6.43 per cent. of the tagged fish is recaptured, overall figures such as this are not very informative and further refinement of this figure is not urgently necessary. The more important aspect is the rate at which the tags are recaptured, especially in relation to the average population from which the fish have been taken and to the rates at which other processes are removing fish from the same population. This section of the programme is still, unfortunately, the most deficient since it has been impossible to ensure that:

(1) All recovered tags are returned with full information on the fish carrying them;

(2) Full statistics on fishing operations in the area (effort and catch) are compiled;

(3) Some measurement is made of the rates of immigration and emigration.

The situation is rendered difficult by the complexity of the patterns of distribution of the fish and fishing operations. Reference is made above and in the earlier paper (Kesteven 1942) to the presence of this species in fresh, brackish, and marine waters. Within this series of habitats there are different ontological facies of the species distribution and each, at least in fish older than I +, is subject to seasonal modulation. In simple terms, the mature fish spend winter and spring in fresh water, summer in moving from fresh through brackish to marine, and at least part of autumn at sea. The fishing operations in the different habitats vary greatly in intensity; fishing is prohibited in certain localities, thus providing sanctuary, and in other localities fishing is persistent and heavy. In view of this complexity the task of measuring the vital statistics of the population is difficult.

Some indication of the *total* mortality rate may be obtained from the longevity of the tags. Appendix I gives the period of absence of each recovered tag, and averages are given in Table 7. The average over all operations was 190 days, and the range is from 0 (capture on the day of release) to 1012 days; the distribution is decidedly skew with a mode between 125 and 200 days and a prolonged tail to the right. This corresponds to the length distribution curves and also is comparable in shape with the general life expectancy curve. It is thought that the 224 recoveries are for present purposes a reasonable sample of the longevity of the populations into which these tags were released and that, despite the obvious necessity for adjusting the figures of absence according to the age of the fish at release and the numerous other factors, the figure of 190 days represents average life expectancy of such fish beyond their average release age. Since the average age at release of the fish of these experiments is computed on the basis of the data in Section II to be about 2.57 yr (nearly 2 yr 7 months), the present result would mean that these fish have a total life expectancy of 3 yr 1 month, which agrees with earlier observations that the majority of fish were caught in their third or fourth year, and this implies a fairly heavy intensity of fishing. The crudity of these calculations is recognized but they are intended only to indicate the lines along which these inquiries may usefully develop. It should be noted, however, that this type of calculation depends, not upon the conditions stipulated above for the direct estimates of rates of capture, but mainly upon the adequacy of returns. Of course if the conditions could be satisfied this type of calculation also would benefit.

VI. Discussion and Conclusions

The earlier understanding of the biology of this species may be summarized briefly as follows:

It is believed that the fish spawn on the coast, in the surf zone, but this has not yet been confirmed for this or any allied species anywhere in the world. Spawning almost certainly takes place in autumn during, or at the end of, a migration undertaken for the purpose. The young fish develop in the estuarine waters, working away from the sea-water towards brackish and perhaps fresh water, and reaching the lakes, broadwaters, and streams some miles from the coast by their third year. In the third year they begin to mature and move towards the estuary during the summer, departing on the spawning migration at the commencement of autumn.

This period may be interrupted by such events as floods or freshets which drive the fish downstream and perhaps to sea; the migration of II + fish in early summer is an occurrence, described as the hardgut run by the industry, whose regularity or determining factors are quite unknown.

During the spawning migration the fish move consistently northward, sometimes in quite extensive movements. In view of this, and of the fact that the fish are II + and older and are mature, it is assumed that some southward movement must occur in the early years. Crude growth rates have been given.

The following features of the movements of the mullet may be regarded as satisfactorily established:

(1) Movement takes place principally in autumn.

(2) Mature and maturing mullet engage in such movement.

(3) At least 45 per cent. and probably not less than 50 per cent. of the population participates in the movement each year.

(4) The movement leaves the travelling fish north of the point from which they started.

(5) Southward movement is possible among these fish after some northward movement, but it rarely if ever leaves such fish south of the point from which they started.

(6) Movement south of the point at which they were spawned must occur during the first 2 yr of life of this species.

(7) Movements may cover relatively great distances and be accomplished at relatively great rates of travel.

(8) In all probability every fish (unless landlocked) migrates at some time, even if the migration is deferred.

(9) Probably each fish migrates a number of times.

(10) Fish from the entire stock of *M. cephalus* on the eastern coast of Australia participate in these movements; i.e. there are no separate, non-migrating units of stock.

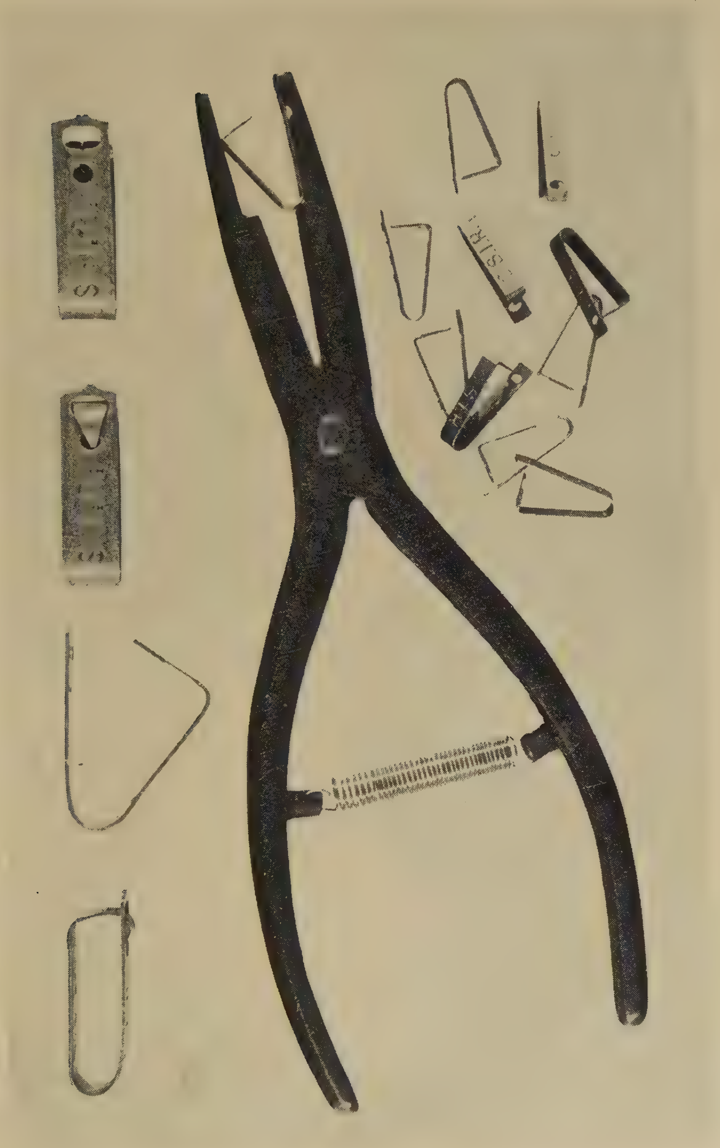
(11) The stock fished commercially in northern waters is drawn in part, if not wholly, from southern waters.

The foregoing is a fairly clear picture of this aspect of the biology of this species. Some points are still obscure, such as when and how southward migration takes place. In general these results show the species to be a euryhaline species living for the first 3 yr predominantly in the coastal systems of rivers and lakes, and then moving to sea in the autumn of the fourth year and each year thereafter, but returning to fresh water within the river system for the greater part of the year; growth takes place in the river system where feeding also occurs.

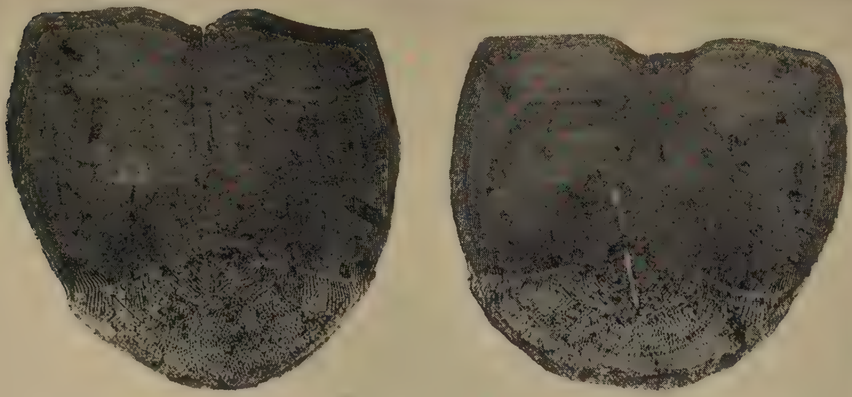
The results on growth may be summarized as follows:

(1) The validity of the interpretation of the features of the scale is confirmed. It is confirmed that breaks are formed annually, dividing the scale into zones whose dimensions are related to the growth of the fish and may be used for calculating rate of growth. Further, the belief that the structural features of the scale are permanent is substantiated.

(2) The earlier results on the rate of growth during the third and fourth year are confirmed.



Pliers and numbered tags used in tagging fish.



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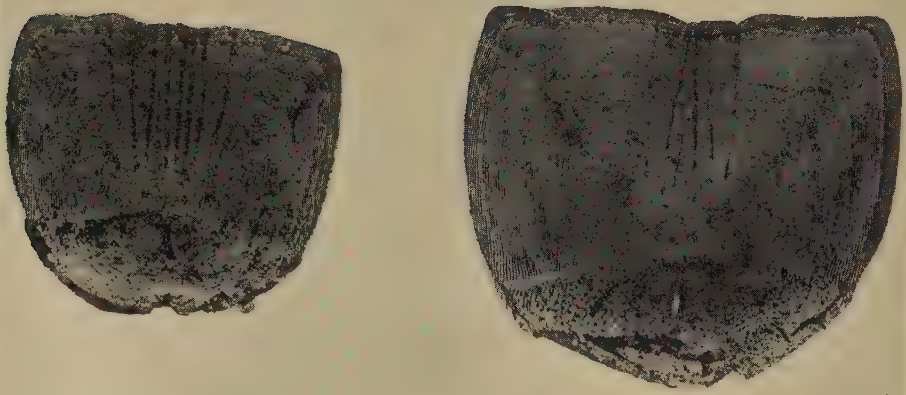

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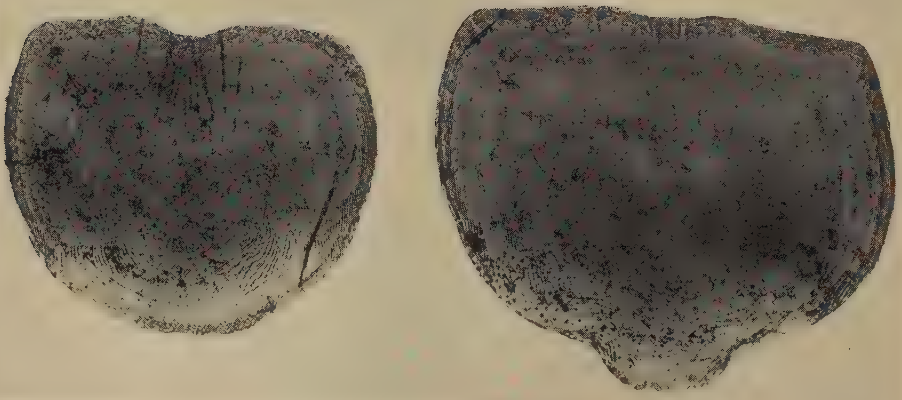

3

Pairs of scales from tagged fish, taken respectively at release (left) and recovery (right). Figures 1, 2, and 3 represent recoveries 102, 210, and 211.

(3) It is shown that growth takes place during part only of the year, probably between October and March.

(4) It is shown that the breaks, which mark off the annuli, are formed in the part of the year when growth takes place, and probably at the commencement of the growth period. Some suggestion is made on the mode of "break" formation.

(5) Some material and tentative ideas are presented on the problems of scale reading.

The results on fishing intensity and natural mortality are most incomplete and can be regarded only as indicating the manner in which this work should develop further.

VII. ACKNOWLEDGMENTS

Since every tagging operation has involved the assistance of a team of fishermen and tagging personnel, almost a different team for each operation, it is impossible to make proper acknowledgment of the help received. One can only express one's thanks and hope that this will come to the notice of those concerned. However, special thanks must be extended to Mr. A. Packer, by whom many of the Port Hacking operations were carried out, and to Dr. H. Thompson, from whom advice and criticism in carrying out the work and in writing this account of its results were received. Thanks are also extended to Mr. D. J. Rochford for advice, criticism, and the hydrological data on Port Hacking.

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APPENDIX I

TAGGING RECOVERIES

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled† (miles)
1	870	5.v.39	Richmond River	44.8	15.vi.39	North Creek, Richmond River	45.0	41	0.2	Nil
2	849	5.v.39	Richmond River	42.2	6.vi.39	Burleigh Head	49.0	32	6.8	*c.* 60
3	812	5.v.39	Richmond River	39.7	29.v.39	Cudgera	39.5	24	—0.2	*c.* 50
4	865	5.v.39	Richmond River	54.7	23.v.39	Cudgera Headland	54.5	18	—0.2	*c.* 50
5	1502	8.ii.40	Clarence River	31.0	8.ii.40	Clarence River	30.5	0	—0.5	Nil
6	1408	8.ii.40	Clarence River	31.5	29.ii.40	Clarence River	30.5	21	—1.0	Nil
7	1420	8.ii.40	Clarence River	29.5	8.ii.40	Clarence River	29.0	0	—0.5	Nil
8	804	5.v.39	Richmond River	38.1	19.xii.39	Lake Cooroibah, Tewantin	39.5	228	1.4	*c.* 250
9	1603	16.xii.39	Nicholson River	42.0	5.iii.40	Melbourne Market	48.0	80	6.0	?
10	1606	16.xii.39	Nicholson River	33.0	25.v.40	Myall Lake	38.0	161	5.0	*c.* 450
11	844	5.v.39	Ballina	40.1	10.vi.40	Brisbane Market	40.2	402	?	?
12	1830	21.vi.40	Tewantin, Noosa River	39.0	23.vi.40	Tewantin	42.0	2	3.0	Nil
13	829	5.v.39	Ballina	39.2	17.vi.40	Tweed Heads	39.2	409	0.0	*c.* 50
14	1488	8.ii.40	Ulmarra	32.5	1.viii.40	Grafton	32.5	175	0.0	Nil
15	1894	21.vi.40	Tewantin, Noosa River	40.0	31.vii.40	Tewantin	41.0	40	1.0	Nil
16	1760	20.vi.40	Entrance to Weyba Lake, Noosa River	32.8	6.ix.40	Weyba Lake	34.3	78	1.5	Nil
17	1870	21.vi.40	Entrance to Noosa River	42.0	14.x.40	Cootharaba Lake		115	?	Nil
18	1880	21.vi.40	Tewantin, Noosa River	43.5	4.ix.40	Noosa Heads		76	?	Nil
19	1815	21.vi.40	Tewantin, Noosa River	38.3	6.xi.40	Weyba Lake	38.7	138	0.4	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
20	1643	13.v.40	Gunnamatta Bay, Port Hacking	29.0	8.xi.40	Cronulla	27.7	179	—1.3	Nil
21	890	9.xi.39	Gunnamatta Bay, Port Hacking	25.0	15.ix.40	Mullet Creek, Hawkesbury River	28.5-31.0	311	Possibly	*c.* 40
22	1092	9.xi.39	Gunnamatta Bay, Port Hacking	23.0	15.ix.40	Mullet Creek, Hawkesbury River		311	5.6	*c.* 40
23	1546	13.v.40	Gunnamatta Bay, Port Hacking	30.0	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
24	1553	13.v.40	Gunnamatta Bay, Port Hacking	30.0	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
25	1555	13.v.40	Gunnamatta Bay, Port Hacking	30.0	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
26	1559	13.v.40	Gunnamatta Bay, Port Hacking	31.0	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
27	1565	13.v.40	Gunnamatta Bay, Port Hacking	29.9	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
28	1566	13.v.40	Gunnamatta Bay, Port Hacking	29.2	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
29	1568	13.v.40	Gunnamatta Bay, Port Hacking	30.1	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
30	1577	13.v.40	Gunnamatta Bay, Port Hacking	30.2	15.ix.40	Mullet Creek, Hawkesbury River		125	?	*c.* 40
31	1578	13.v.40	Gunnamatta Bay, Port Hacking	29.8	15.ix.40	Hawkesbury River		125	?	*c.* 40
32	1579	13.v.40	Gunnamatta Bay, Port Hacking	26.6	15.ix.40	Hawkesbury River		125	?	*c.* 40
33	1580	13.v.40	Gunnamatta Bay, Port Hacking	30.9	15.ix.40	Hawkesbury River		125	?	*c.* 40

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
34	1586	13.v.40	Gunnamatta Bay, Port Hacking	32.8	15.ix.40	Hawkesbury River		125	?	*c.* 40
35	1588	13.v.40	Gunnamatta Bay, Port Hacking	28.0	15.ix.40	Hawkesbury River		125	?	*c.* 40
36	1591	13.v.40	Gunnamatta Bay, Port Hacking	30.4	15.ix.40	Hawkesbury River		125	?	*c.* 40
37	1592	13.v.40	Gunnamatta Bay, Port Hacking	31.2	15.ix.40	Hawkesbury River		125	?	*c.* 40
38	1595	13.v.40	Gunnamatta Bay, Port Hacking	29.7	15.ix.40	Hawkesbury River		125	?	*c.* 40
39	1621	13.v.40	Gunnamatta Bay, Port Hacking	31.1	15.ix.40	Hawkesbury River		125	?	*c.* 40
40	1625	13.v.40	Gunnamatta Bay, Port Hacking	28.4	15.ix.40	Hawkesbury River		125	?	*c.* 40
41	1626	13.v.40	Gunnamatta Bay, Port Hacking	32.9	15.ix.40	Hawkesbury River		125	?	*c.* 40
42	1635	13.v.40	Gunnamatta Bay, Port Hacking	25.4	15.ix.40	Hawkesbury River		125	?	*c.* 40
43	1640	13.v.40	Gunnamatta Bay, Port Hacking	28.7	15.ix.40	Hawkesbury River		125	?	*c.* 40
44	1647	13.v.40	Gunnamatta Bay, Port Hacking	31.4	15.ix.40	Hawkesbury River		125	?	*c.* 40
45	1650	13.v.40	Gunnamatta Bay, Port Hacking	29.2	15.ix.40	Hawkesbury River		125	?	*c.* 40
46	1653	13.v.40	Gunnamatta Bay, Port Hacking	31.3	15.ix.40	Hawkesbury River		125	?	*c.* 40
47	1656	13.v.40	Gunnamatta Bay, Port Hacking	31.0	15.ix.40	Hawkesbury River		125	?	*c.* 40

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture				Interim	
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	(cm) Growth	Distance Travelled (miles)
48	1658	13.v.40	Gunnamatta Bay, Port Hacking	28.1	15.ix.40	Hawkesbury River		125	?	*c.* 40
49	1667	13.v.40	Gunnamatta Bay, Port Hacking	31.9	15.ix.40	Hawkesbury River		125	?	*c.* 40
50	1672	13.v.40	Gunnamatta Bay, Port Hacking	28.2	15.ix.40	Hawkesbury River		125	?	*c.* 40
51	1677	13.v.40	Gunnamatta Bay, Port Hacking	30.8	15.ix.40	Hawkesbury River		125	?	*c.* 40
52	1684	13.v.40	Gunnamatta Bay, Port Hacking	29.8	15.ix.40	Hawkesbury River		125	?	*c.* 40
53	1709	13.v.40	Gunnamatta Bay, Port Hacking	29.9	15.ix.40	Hawkesbury River		125	?	*c.* 40
54	1780	20.vi.40	Entrance to Weyba Lake, Noosa River	34.1	26.xii.40	Lake Cooroibah	35.0	189	0.9	Nil
55	1907	21.vi.40	Tewantin, Entrance to Noosa River	37.2	6.i.41	Weyba Lake	45.0	199	7.8	Nil
56	1772	20.vi.40	Entrance to Weyba Lake, Noosa River	37.2	7.i.41	Weyba Lake	39.5	201	2.3	Nil
57	2232	11.i.41	Lake Illawarra	23.0	Jan. 41	Lake Illawarra	24.0	?	1.0	Nil
58	2668	20.iii.41	Lake Macquarie	30.1	23.iii.41	Lake Macquarie	30.5	3	0.4	Nil
59	2325	20.iii.41	Lake Macquarie	38.2	25.iii.41	Lake Macquarie	?	5	?	Nil
60	1768	20.vi.40	Entrance to Weyba Lake, Noosa River	41.6	20.iii.41	Noosa River	48.3	273	6.7	Nil
61	2593	19.iii.41	Hawkesbury River	22.0	10.iv.41	Mangrove Creek	?	22	?	Nil
62	2735	6.v.41	Richmond River	21.6	22.v.41	Ballina	?	16	?	Nil-released
63	2892	15.v.41	Terranora Creek	25.6	3.vi.41	Tweed River	28.0	19	2.4	Nil
64	1921	21.vi.40	Entrance to Noosa River, Tewantin	31.9	12.vi.41	Tewantin	37.0	356	5.1	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
65	2259	11.i.41	Lake Illawarra	26.0	16.vi.41	Dapto	28.8	156	2.8	Nil
66	2762	8.v.41	Terranora Creek	30.7	19.vi.41	Caloundra	29.0	42	—1.7	*c.* 140
67	1750	20.vi.40	Entrance to Weyba Lake, Noosa River	33.8	2.vii.41	Tin Can Bay	34.1	377	—0.3	*c.* 70
68	2794	11.v.41	Noosa River	26.5	3.vii.41	Fraser I.	31.8	53	5.3	*c.* 100
69	1898	21.vi.40	Noosa River	43.0						
70	1715	20.vi.40	Entrance to Weyba Lake, Noosa River	34.2	1.vi.41	Noosa River	33.8	346	—0.4	Nil
71	2782	8.v.41	Terranora Creek	32.2	13.vi.41	Tweed River		36		Nil
72	2891	15.v.41	Terranora Creek	23.0	13.vi.41	Terranora Broadwater	22.3	29	—0.7	Nil
73	2780	8.v.41	Terranora Creek	36.7			34.4		—2.3	
74	2843	15.v.41	Terranora Creek	22.4	7.viii.41	Terranora Creek	22.5	84	—0.2	Nil
75	2920	15.v.41	Terranora Creek	23.5	12.viii.41	Fingal, Tweed River	24.0	89	0.5	Nil
76	2833	15.v.41	Terranora Creek	23.8	12.viii.41	Fingal, Tweed River	23.5	89	—0.3	Nil
77	2863	15.v.41	Terranora Creek	23.1	4.ix.41	Tweed Heads	26.0	112	2.9	Nil
78	2789	11.v.41	Noosa River	41.0	19.viii.41	Noosa River	41.0	100	—0.0	Nil
79	2884	15.v.41	Terranora Creek	25.8	19.x.41	Tweed River	26.2	157	0.4	Nil
80	2887	15.v.41	Terranora Creek	22.2	30.x.41	Terranora Creek	24.0	168	1.8	Nil
81	2916	15.v.41	Terranora Creek	26.1	17.xi.41	Junction of Tweed River and Terranora Creek	27.1	186	1.0	Nil
82	2461	24.ii.41	Port Hacking	27.3	27.xi.41	Port Hacking	32.2	276	4.9	Nil
83	2897	15.v.41	Terranora Creek	23.3	7.xii.41	Terranora Creek	29.2	206	5.9	Nil
84	2239	11.i.41	Lake Illawarra	23.7	7.i.42	Lake Illawarra	28.2	361	4.5	Nil
85	2744	6.v.41	Richmond River	28.1	22.i.41	Tweed River	30.0		1.9	*c.* 50
86	3130	1.xii.41	Port Hacking	25.7	25.ii.42	Port Hacking	27.6	86	1.9	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
87	2849	15.v.41	Terranora Creek	23.9	2.iii.42	Tweed River	29.2	291	5.3	Nil
88	2856	15.v.41	Terranora Creek	27.3	2.iii.42	Tweed River	30.7	291	3.4	Nil
89	2939	16.v.41	Currumbin Creek	21.5	10.iii.42	Southport	26.0		4.5	25
90	2908	15.v.41	Terranora Creek	23.2	24.iii.42	Cobaki Bridge	30.5	313	7.3	Nil
91	2515	24.ii.41	Port Hacking	24.9	14.iv.42	Camden Haven	36.0	414	11.1	250
92	3002	16.v.41	Currumbin Creek	24.8	24.iv.42	8 Miles from Southport	32.7	343	7.9	25
93	2319	20.iii.41	Lake Macquarie	38.0	15.v.42	Richmond River	41.9	421	3.9	300
94	3020	16.v.41	Currumbin Creek	23.7	26.v.42	Coomera River	33.1	375	9.4	25
95	2390	20.iii.41	Lake Macquarie	33.4	12.v.42	3 Miles N. of N.S.W. border	34.5	418	1.1	350
96	3042	16.v.41	Currumbin Creek	25.3	5.ix.42	Tweed River	30.5	477	5.2	Nil
97	146	25.vi.42	Port Hacking	31.6	29.x.42	Port Hacking	31.9	126	0.3	Nil
98	229	25.vi.42	Port Hacking	31.4	29.x.42	Port Hacking	31.8	126	0.4	Nil
99	127	25.vi.42	Port Hacking	31.4	10.xii.42	Port Hacking	31.8	168	0.4	Nil
100	275	25.vi.42	Port Hacking	28.0	10.xii.42	Port Hacking	28.7	168	0.7	Nil
101	354	29.x.42	Gunnamatta Bay, Port Hacking	27.0	10.xii.42	Port Hacking	27.0	42	0.0	Nil
102	137	25.vi.42	Port Hacking	31.0	31.xii.42	Port Hacking	32.2	189	1.2	Nil
103	247	25.vi.42	Port Hacking	27.1	31.xii.42	Port Hacking	28.1	189	1.0	Nil
104	4159	5.i.43	Fisherman's Bay, Port Hacking	31.9	20.i.43	Port Hacking	32.0	15	0.1	Nil
105	308	25.vi.42	Port Hacking	27.1	3.ii.43	Port Hacking	29.5	223	2.4	Nil
106	4021	5.i.43	Fisherman's Bay, Port Hacking	29.0	3.ii.43	Port Hacking	29.4	29	0.4	Nil
107	4076	5.i.43	Fisherman's Bay, Port Hacking	26.6	3.ii.43	Port Hacking	26.7	29	0.1	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
108	4104	5.i.43	Fisherman's Bay, Port Hacking	32.0	3.ii.43	Port Hacking	32.0	29	0.0	Nil
109	171	25.vi.42	Port Hacking	30.9	4.ii.43	Port Hacking	33.8	224	2.9	Nil
110	361	29.x.42	Gunnamatta Bay, Port Hacking	30.3	4.ii.43	Port Hacking	31.1	98	0.8	Nil
111	58	30.v.42	Port Macquarie	31.4	16.i.43	Port Macquarie	33.7	231	2.3	
112	3216	3.ii.43	Sandspit, Port Hacking	32.1	4.ii.43	Jervis Bay	32.1	1	0.0	120‡
113	4196	4.ii.43	Sandspit, Port Hacking	30.6	7.ii.43	Port Hacking	30.6	3	0.0	Nil
114	4154	5.i.43	Fisherman's Bay, Port Hacking	28.7	4.iii.43	Port Hacking	28.5	58	—0.2	Nil
115	4158	5.i.43	Fisherman's Bay, Port Hacking	31.5	4.iii.43	Port Hacking	31.4	58	—0.1	Nil
116	3246	3.ii.43	Sandspit, Port Hacking	27.5	4.iii.43	Port Hacking	27.8	29	0.3	Nil
117	3249	3.ii.43	Sandspit, Port Hacking	28.4	4.iii.43	Port Hacking	28.1	29	—0.3	Nil
118	3264	3.ii.43	Sandspit, Port Hacking	33.0	4.iii.43	Port Hacking	32.7	29	—0.3	Nil
119	3268	3.ii.43	Sandspit, Port Hacking	33.5	4.iii.43	Port Hacking	33.6	29	0.1	Nil
120	3272	3.ii.43	Sandspit, Port Hacking	28.8	4.iii.43	Port Hacking	28.5	29	—0.3	Nil
121	2947	16.v.41	Currumbin Creek	23.2	3.iii.43	Logan River	34.4	656	11.2	40
122	2300	19.iii.41	Hawkesbury River	19.9	19.iii.43	Port Hacking	*c.* 30.0	730	*c.* 10.0	70-released

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
123	3398	4.ii.43	Sandspit, Port Hacking	32.0	19.iii.43	Port Hacking	31.6	43	—0.4	Nil-released
124	3243	3.ii.43	Sandspit, Port Hacking	34.5	26.iii.43	Port Hacking	35.2	51	0.7	Nil
125	4256	19.iii.43	Gunnamatta Bay, Port Hacking	30.6	29.iii.43	Port Hacking	30.6	10	0.0	Nil
126	3250	3.ii.43	Sandspit, Port Hacking	28.2	27.iii.43	Port Hacking	29.2	52	1.0	Nil
127	270	25.vi.42	Sandspit, Port Hacking	25.0	8.iv.43	Port Hacking	29.5	287	4.5	Nil-released
128	4169 or 4160	5.i.43	Fisherman's Bay, Port Hacking		8.iv.43	Port Hacking	30.9	93	Nil	Released
129	3218	3.ii.43	Sandspit, Port Hacking	28.8	8.iv.43	Port Hacking	31.0	64	2.2	Nil
130	3222	3.ii.43	Sandspit, Port Hacking	31.7	8.iv.43	Port Hacking	32.5	64	0.8	Nil
131	3227	3.ii.43	Sandspit, Port Hacking	31.6	8.iv.43	Port Hacking	31.8	64	0.2	Nil
132	3242	3.ii.43	Sandspit, Port Hacking	30.3	8.iv.43	Port Hacking	31.7	64	1.4	Nil
133	4175	5.i.43	Fisherman's Bay, Port Hacking	31.2	8.iv.43	Port Hacking	33.0	93	1.8	Nil
134	4177	5.i.43	Fisherman's Bay, Port Hacking	31.5	8.iv.43	Port Hacking	32.6	93	1.1	Nil
135	4364	8.iv.43	Fisherman's Bay, Port Hacking	27.5	28.v.43	Port Hacking	27.5	50	0.0	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
136	4386	8.iv.43	Fisherman's Bay, Port Hacking	30.0	28.v.43	Port Hacking	30.0	50	0.0	Nil
137	4409	8.iv.43	Fisherman's Bay, Port Hacking	30.0	28.v.43	Port Hacking	29.7	50	—0.3	Nil
138	4138	5.i.43	Fisherman's Bay, Port Hacking	29.8	28.v.43	Port Hacking	30.7	143	0.9	Nil
139	3269	3.ii.43	Sandspit, Port Hacking	35.0	28.v.43	Port Hacking	37.1	114	2.1	Nil
140	4399	8.iv.43	Fisherman's Bay, Port Hacking	28.9	28.v.43	Port Hacking	28.9	50	0.0	Nil
141	4470	15.iv.43	Gunnamatta Bay, Port Hacking	34.5	28.v.43	Port Hacking	34.3	43	—0.2	Nil
142	3236	3.ii.43	Sandspit, Port Hacking	28.2	28.v.43	Port Hacking	30.1	114	1.9	Nil
143	4153	5.i.43	Fisherman's Bay, Port Hacking	32.2	28.v.43	Port Hacking	32.8	143	0.6	Nil
144	4080	5.i.43	Fisherman's Bay, Port Hacking	30.2	28.v.43	Port Hacking	31.8	143	1.6	Nil
145	4329	8.iv.43	Fisherman's Bay, Port Hacking	25.0	28.v.43	Port Hacking	25.0	50	0.0	Nil
146	4161	5.i.43	Fisherman's Bay, Port Hacking	30.7	28.v.43	Port Hacking	32.6	143	1.9	Nil
147	4401	8.iv.43	Fisherman's Bay, Port Hacking	29.1	28.v.43	Port Hacking	28.7	50	—0.4	Nil
148	4408	8.iv.43	Fisherman's Bay, Port Hacking	28.3	28.v.43	Port Hacking	28.5	50	0.2	Nil
149	4267	19.iii.43	Gunnamatta Bay, Port Hacking	35.0	28.v.43	Port Hacking	34.5	70	—0.5	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
150	308	3.ii.43	Sandspit, Port Hacking	29.5	28.v.43	Port Hacking	30.4	114	0.9	Nil
151	4283	19.iii.43	Gunnamatta Bay, Port Hacking	34.3	28.v.43	Port Hacking	33.7	70	—0.6	Nil
152	4424	8.iv.43	Fisherman's Bay, Port Hacking	28.7	28.v.43	Port Hacking	28.9	50	0.2	Nil
153	2366	20.iii.41	Lake Macquarie	34.0	20.v.43	Clarence River	39.4	791	5.4	260
154	4356	8.iv.43	Fisherman's Bay, Port Hacking	29.3	28.v.43	Port Hacking	29.3	50	0.0	Nil
155	4454	15.iv.43	Gunnamatta Bay, Port Hacking	39.3	27.v.43	Southport	39.2	42	—0.1	460
156	2296	11.i.41	Lake Illawarra	24.1	9.vi.43	Grafton	43.8	879	19.7	350
157	3031	16.v.41	Currumbin Creek	20.5	29.vi.43	Cape Moreton	—	774	—	63
158	4069	5.i.43	Fisherman's Bay, Port Hacking	30.0	7.vii.43	Wallis Lake	35.0	183	5.0	210
159	2230	11.i.41	Lake Illawarra	23.3	3.viii.43	Tweed Heads	36.9	934	13.6	420
160	391	5.i.43	Fisherman's Bay, Port Hacking	30.2	14.ix.43	Port Hacking	33.2	252	3.0	Nil
161	3214	3.ii.43	Sandspit, Port Hacking	29.2	14.ix.43	Port Hacking	30.3	223	1.1	Nil
162	3230	3.ii.43	Sandspit, Port Hacking	29.2	14.ix.43	Port Hacking	30.3	223	1.1	Nil
163	4095	5.i.43	Fisherman's Bay, Port Hacking	30.5	14.ix.43	Port Hacking	32.0	252	1.5	Nil-released
164	4177	8.iv.43	Fisherman's Bay, Port Hacking	32.6 (2nd recapture, see 134)	14.ix.43	Port Hacking	32.8	159	0.2	Nil-released

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
165	4222	19.iii.43	Gunnamatta Bay, Port Hacking	33.8	14.ix.43	Port Hacking	37.4	179	3.6	Nil
166	4238	19.iii.43	Gunnamatta Bay, Port Hacking	34.5	14.ix.43	Port Hacking	34.1	179	—0.4	Nil-released
167	4261	19.iii.43	Gunnamatta Bay, Port Hacking	37.5	14.ix.43	Port Hacking	37.8	179	0.3	Nil
168	4368	8.iv.43	Fisherman's Bay, Port Hacking	28.7	14.ix.43	Port Hacking	29.0	159	0.3	Nil-released
169	4402	8.iv.43	Fisherman's Bay, Port Hacking	28.7	14.ix.43	Port Hacking	28.8	159	0.1	Nil
170	4370	8.iv.43	Fisherman's Bay, Port Hacking	25.0	14.ix.43	Port Hacking	27.1	159	2.1	Nil
171	4390	8.iv.43	Fisherman's Bay, Port Hacking	29.9	14.ix.43	Port Hacking	30.4	159	0.5	Nil
172	3312	4.ii.43	Sandspit, Port Hacking	33.5	14.ix.43	Port Hacking	33.0	222	—0.5	Nil
173	4127	5.i.43	Fisherman's Bay, Port Hacking	32.5	14.ix.43	Port Hacking	32.5	252	0.0	Nil
174	4428	15.iv.43	Gunnamatta Bay, Port Hacking	38.6	10.ix.43	Putty Beach, N. of Botany Bay		148		45
175	4321	19.iii.43	Gunnamatta Bay, Port Hacking	34.1	26.ix.43	Yowie Bay		191		Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
176	3214	14.ix.43	Fisherman's Bay, Port Hacking	30.3	11.x.43	Yowie Bay	30.3	27	0.0	Nil-released
				(2nd recapture, see 161)						
177	3307	4.ii.43	Sandspit, Port Hacking	29.6	11.x.43	Yowie Bay	31.2	249	1.6	Nil-released
178	4020	5.i.43	Fisherman's Bay, Port Hacking	29.9	11.x.43	Yowie Bay	33.5	279	3.6	Nil
179	4070	5.i.43	Fisherman's Bay, Port Hacking	29.7	11.x.43	Port Hacking	31.0	279	1.3	Nil
180	4121	5.i.43	Fisherman's Bay, Port Hacking	32.0	11.x.43	Port Hacking	32.6	279	0.6	Nil-released
181	4129	5.i.43	Fisherman's Bay, Port Hacking	30.0	11.x.43	Port Hacking	31.4	279	1.4	Nil
182	4257	19.iii.43	Gunnamatta Bay, Port Hacking	34.9	11.x.43	Port Hacking	34.6	206	—0.3	Nil
183	4328	8.iv.43	Fisherman's Bay, Port Hacking	25.1	11.x.43	Port Hacking	25.0	186	—0.1	Nil
184	4355	8.iv.43	Fisherman's Bay, Port Hacking	26.2	11.x.43	Port Hacking	26.7	186	0.5	Nil
185	4413	8.iv.43	Fisherman's Bay, Port Hacking	29.5	11.x.43	Port Hacking	29.1	186	—0.4	Nil
186	4418	8.iv.43	Fisherman's Bay, Port Hacking	34.1	11.x.43	Port Hacking	34.4	186	0.3	Nil
187	4448	15.iv.43	Gunnamatta Bay, Port Hacking	37.2	11.x.43	Port Hacking	37.2	179	0.0	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
188	4487	15.iv.43	Gunnamatta Bay, Port Hacking	35.9	11.x.43	Port Hacking	35.7	179	—0.2	Nil
189	509	14.ix.43	Fisherman's Bay, Port Hacking	32.9	11.x.43	Port Hacking	33.0	27	0.1	Nil-released
190	558	14.ix.43	Fisherman's Bay, Port Hacking	33.1	11.x.43	Port Hacking	32.7	27	—0.4	Nil-released
191§	4250	19.iii.43	Gunnamatta Bay, Port Hacking	32.6	20.iii.43	Port Hacking	32.6	1	0.0	Nil
192	31	28.v.42	Port Macquarie	20.7	10.xi.43	Port Macquarie	28.6	531	7.9	Nil
193	573	14.ix.43	Fisherman's Bay, Port Hacking	28.3	28.xi.43	Port Hacking	28.6	75	0.3	Nil
194	4528	18.viii.43	Near Mitchell's Boatshed, Southport beach	23.1	12.xi.43	Southport	24.0	86	0.9	Nil-released
195	4552	2.xi.43	Nerang River, Southport	21.7	18.i.43	Jumpinpin	26.0	77	4.3	Nil
196	4693	18.viii.43	Mitchell's Boatshed, Southport	23.1	2.xi.43	Southport	24.6	76	1.5	Nil-released
197	4694	18.viii.43	Mitchell's Boatshed, Southport	21.5	2.xi.43	Southport	22.5	76	1.0	Nil-released
198	4697	18.viii.43	Mitchell's Boatshed, Southport	22.1	2.xi.43	Southport	22.6	76	0.5	Nil
199	4694	2.xi.43	Nerang River, Southport	22.5	24.i.44	Southport	27.2	83	4.7	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
200	694	11.x.43	Fisherman's Bay, Port Hacking	30.2	8.ii.44	Port Hacking	33.2	120	3.0	Nil
201	4689	18.viii.43	Nerang River, Southport	22.4	16.iii.44	Southport	30.4	211	8.0	Nil
202	656	11.x.43	Fisherman's Bay, Port Hacking	36.2	4.vii.44	Myall Lakes	37.0	267	0.8	190
203	4307	19.iii.43	Gunnamatta Bay, Port Hacking	35.9	2.vi.44	Boat Harbour	40.5	441	4.6	6
204	4352	8.iv.43	Fisherman's Bay, Port Hacking	24.6	5.viii.44	Port Hacking	30.0	485	5.4	Nil
205	4107	5.i.43	Fisherman's Bay, Port Hacking	30.4	17.viii.44	Port Hacking	36.0	590	5.6	Nil
206	588	14.ix.43	Fisherman's Bay, Port Hacking	29.3	17.viii.44	Port Hacking	33.0	338	3.7	Nil
207	757	11.x.43	Fisherman's Bay, Port Hacking	34.0	17.viii.44	Port Hacking	37.0	311	3.0	Nil
208	604	14.ix.43	Fisherman's Bay, Port Hacking	32.9	24.viii.44	Port Hacking	36.5	345	3.6	Nil
209	662	11.x.43	Fisherman's Bay, Port Hacking	31.8	30.viii.44	Port Hacking	37.0	324	5.2	Nil
210	4375	8.iv.43	Fisherman's Bay, Port Hacking	24.1	30.viii.44	Port Hacking	33.0	510	8.9	Nil
211	4273	19.iii.43	Gunnamatta Bay, Port Hacking	28.0	5.ix.44	Port Hacking	35.1	536	7.1	Nil
212	570	14.ix.43	Fisherman's Bay, Port Hacking	22.5	5.ix.44	Port Hacking	36.4	357	13.9	Nil
213	756	11.x.43	Fisherman's Bay, Port Hacking	30.4	5.ix.44	Port Hacking	36.0	330	5.6	Nil

APPENDIX I (*Continued*)

Recovery No.	Tag No.	Release			Recapture			Interim		
		Date	Place	Length (cm)	Date	Place	Length (cm)	Days	Growth (cm)	Distance Travelled (miles)
214	780	11.x.43	Fisherman's Bay, Port Hacking	28.4	5.ix.44	Port Hacking	33.7	330	5.3	Nil
215	623	14.ix.43	Fisherman's Bay, Port Hacking	29.3	6.ix.44	Port Hacking	35.2	358	5.9	Nil
216	4588	2.xi.43	Nerang River, Southport	21.4	2.ix.44	Southport	29.1	305	7.7	Nil
217	553	14.ix.43	Fisherman's Bay, Port Hacking	32.7	15.ix.44	Port Hacking	36.1	367	3.4	Nil
218	539	14.ix.43	Fisherman's Bay, Port Hacking	22.7	15.ix.44	Port Hacking	30.7	367	8.0	Nil
219	394	5.i.43	Fisherman's Bay, Port Hacking	28.4	15.ix.44	Port Hacking	37.2	619	8.8	Nil
220	774	11.x.43	Fisherman's Bay, Port Hacking	31.2	18.ix.44	Port Hacking	35.0	343	3.8	Nil
221	654	11.x.43	Fisherman's Bay, Port Hacking	31.5	19.xi.44	Port Hacking	35.2	405	3.7	Nil
222	708	11.x.43	Fisherman's Bay, Port Hacking	31.5	15.ii.45	Port Hacking	38.2	493	6.7	Nil
223	4289	19.iii.43	Gunnamatta Bay, Port Hacking	31.0	29.iii.45	Botany Bay	Not given	741	?	10
224	513	14.ix.43	Fisherman's Bay, Port Hacking	31.8	22.vi.46	Ballina	41.3	1012	9.5	375

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* The places under "Recapture" are generally those given by the person returning the tag, and mostly refer to localities rather than precise points. Generally, therefore, where the locality named is the same as where the fish was released, distance travelled is recorded as nil. This procedure is consistent with recognition of the fact that travel within a system of waters (a river with its tributaries, lakes, etc.) is not measurable.

† The note "released" in this column indicates that the tagged fish were measured and released again at once.

‡ See discussion in Section V(*a*) (i). § Injured fish.

DISTRIBUTION OF MARINE INVERTEBRATES BY SHIPS

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Summary

In comparatively recent years a number of sedentary marine invertebrates have been found on the east coast of Australia, where they were previously unknown. New records for Australian waters are:

Bryozoa—*Bugula flabellata* Thompson, *Conopeum tubigerum* Osburn, *Schizoporella unicornis* Johnston, *Watersipora cucullata* Busk, and *Anguinella palmata* van Beneden;

Polychaeta (Serpulidae)—*Mercierella enigmatica* Fauvel;

Cirripedia—*Balanus algicola* Pilsbry.

By reason of their abundance, these species could not have been overlooked by field collectors, and as they are ship-fouling organisms in other parts of the world it is concluded that they have been introduced by ships.

An examination is made of the factors militating against such importations, but despite the difficulties encountered, organisms can be successfully translocated by ships. Mention is made of some of the more outstanding introductions that have occurred overseas in recent years. The available evidence suggests that many cosmopolitan species may owe their wide distribution to the movements of shipping.

I. INTRODUCTION

During studies on the fouling of submerged surfaces a number of organisms have been observed which have not been recorded previously from Australia. Many of these are common in other parts of the world, but were either previously absent from the Australian fauna or overlooked by earlier workers.

This paper discusses the probable introduction of some of these species and considers the question of translocation of sessile marine organisms in general. References to the distribution of individual organisms by the movements of shipping are frequent in systematic literature, yet comparatively little attention seems to have been given to this aspect of the fouling problem. In recent years the classic instance of the introduction of an Australian barnacle into British waters has focused more attention on the possibility of other undesirable importations.

All identifications were made initially by the author, but the barnacles were checked subsequently by Miss E. Pope of the Australian Museum, and the serpulids by Miss B. Dew, Division of Fisheries, C.S.I.R.O. All necessary references were consulted in determining the Bryozoa, and specimens were compared with those in the Australian Museum collection, Sydney. The identification of the nudibranch *Thecacera pennigera* Montagu was confirmed by Miss J. K. Allan of the Australian Museum. Specimens of all material have been lodged in this museum.

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II. RESULTS

The occurrence of some species of Bryozoa in Australian waters is recorded here for the first time. The fact that some of these species are now predominant in the local fauna, where they were previously unknown, is significant. This is especially true of *Watersipora cucullata* Busk 1854 (Hastings 1930) which is now the most abundant shallow-water bryozoan on the New South Wales coast. It has also been found as far afield as Fremantle, Port Adelaide, and at a number of points along the Queensland coast from Moreton Bay to Thursday I. Haswell made no mention of it in his numerous papers, nor did Whitelegge (1889), and Dakin (personal communication) knew it initially only from the Watson's Bay area of Sydney Harbour; yet now it is very widely distributed. As it is known from regions to the north and west of Australia, its distribution might be ascribed to currents were it not that, on present knowledge, it has so far failed to appear in some intermediate localities. As it is exceedingly copper-tolerant and can exist attached to fast ships for months, the evidence suggests ship transport.

Another species very common on the New South Wales coast is *Bugula flabellata* Thompson 1847 (Hincks 1880). A fouling organism from the Atlantic and Mediterranean regions, it now ranges from Eden north to Port Stephens on this coast; it is also established in Port Adelaide (Outer Harbour). Small encrusting zoaria of *Schizoporella unicornis* Johnston 1847 (Hincks 1880) were recorded from the Great Barrier Reef some years ago but the massive forms of this species, not seen on the Reef, are now abundant as fouling organisms in both Port Jackson and Fremantle Harbour. There is evidence that this species arrived in Sydney on two small Japanese vessels which were captured and anchored in Watson's Bay during the war, and that it spread throughout Port Jackson from this focus.

Two more species of Bryozoa new to the Australian fauna are much more restricted in their local range. One, believed to be *Anguinella palmata* van Beneden 1844 (Hincks 1880), known only from the Atlantic, was found to be flourishing in the harbour at Newcastle, N.S.W. The other, *Conopeum tubigerum* Osburn (Osburn 1940), which was described from the West Indies as recently as 1940, has to date been found only on fouling plates at Townsville, Queensland.

Serpulid worms are one of the most important groups of fouling organisms and provide several points of interest. *Mercierella enigmatica* Fauvel is a brackish-water form which has been recorded from the Swan River, W.A. (Monro 1938*b*). However, recent specimens and information indicate that it ranges around at least the southern half of the Australian continent, from Noosa, Queensland, to Carnarvon, W.A. In many of the localities where it is now abundant it was previously unknown.

A surprising discovery was that of the British nudibranch *Thecacera pennigera* Montagu (Alder and Hancock 1855) in the upper reaches of Sydney Harbour. Specimens were obtained on two occasions by Miss B.

Dew, Division of Fisheries, C.S.I.R.O., during the course of sea-water conduit inspections at White Bay Power Station. To the writer's knowledge this constitutes the first record of this species outside British waters.

The barnacle *Balanus algicola* Pilsbury 1916 is another addition to our fauna. It is found on the New South Wales coast, being fairly common throughout its range from Eden to Port Stephens.

While the foregoing species are by no means all the new records established during the last few years, they have been selected as further evidence to support the theory that organisms can be translocated by ships.

III. Discussion

The most obvious ways in which sedentary marine organisms can be transferred to new localities are as larvae borne by ocean currents or as adults carried on submerged surfaces, to a locality favourable for their development. The movement of larvae would be governed by the speed and direction of the current and the time of larval development. Such a movement south along the east coast of Australia would be possible (Koninklijk Nederlands Meteorologische Instituut 1949). If it did occur there would be a steady and continuous migration, the organism occupying each favourable locality in turn as it moved south. There is evidence to suggest that, to a limited extent, this does occur.

For adults ships would constitute the main submerged surfaces involved, and we should expect, provided the environment were favourable, the greatest assortment of fouling organisms in the larger ports, and also that there would be a discontinuity in occurrence. Both these conditions operate in eastern Australia, strongly suggesting that shipping is the chief translocating agency. A number of objections to the second theory, however, could be raised:

(1) The number of organisms required to establish a new population must be more than a few isolated individuals, so that the introduction can compete with an already established fauna.

(2) The larval stages of the organism must settle in large numbers on a ship's bottom whilst it is in port. For this to happen, any antifouling measures must be ineffective against the organism concerned.

(3) The immature organisms must survive the rigours of a voyage, of being subjected to strong currents which would reduce the efficiency of their feeding mechanisms and which in more delicate forms may mechanically remove insecurely attached juveniles. Further, the vessel may pass through waters of temperature and salinity outside the normal range of tolerance of the organism concerned.

(4) When the vessel reaches another port not only must the environment be favourable but the organism must either be, or have time to become, sexually mature and reproduce, and the larvae must establish themselves in competition with local forms.

In the face of these objections, the probability of an organism surviving a voyage on a ship's bottom, the first essential of a successful translocation, seems to be very slight. The question remained in dispute for many years, and even as late as 1928 Visscher wrote: "It has long been a debated question whether a given species of barnacle or other organism attached to the bottom of a boat can survive transportation to another port and continue to live and reproduce its kind. Whether one can explain the mundane distribution of some species of organisms in this manner never has been determined."

The writer has examined the hulls of many naval vessels and has found that the serpulid *Hydroides norvegica* Gunnerus and the bryozoan *Watersipora cucullata* Busk will survive a 3-months' cruise through tropical, warm temperate, and cool temperate waters at speeds up to 30 kt. Further, aircraft carriers and other vessels which had returned from service in Korean and Japanese waters carried living specimens of the barnacles *Balanus amphitrite albicostatus* Pilsbry, *B. tintinnabulum rosa* Pilsbry, and *B. tintinnabulum volcano* Pilsbry. As far as is known, these barnacles are restricted to Japanese seas. Although somewhat damaged in removal from the hull, specimens of all three survived for weeks in the aquarium before being preserved.

Bishop (1947) has recorded similar observations on barnacles. In one instance he found living *Elminius modestus* Darwin, *Balanus amphitrite* Darwin, and *B. trigonus* Darwin, all common in Australian waters, on the hull of the M.V. "Waipawa" at Liverpool after a passage of 30 days at 17 kt. This ship had been in Australian and New Zealand waters and had returned to Liverpool via the freshwater lakes of the Panama Canal.

These examples show that at least some Bryozoa, barnacles, and serpulids can survive fast voyages over long distances with rapid changes of water conditions.

If the shipping theory is correct, one should find in Sydney Harbour a large assemblage of fouling organisms, for there are high water temperatures, a high degree of pollution with organic matter, and a slow turn-round of shipping. In point of fact one does find this and one suspects strongly that many of the dominant foulers have been imported. It is instructive to consider evidence on individual organisms.

A common fouling hydroid, *Bougainvillia ramosa* van Beneden, was first seen in Watson's Bay, Port Jackson, in 1918 by Briggs (1931), who over a period of years observed its gradual spread throughout the Port.

When recording this addition to the fauna he suggested that it could only have been brought here on the bottom of a ship. Its introduction may have occurred much earlier than this, since Lendenfeld (1885) noted: "I have found some *Bougainvillias* in Port Jackson, which are similar to *B. ramosa*. They are the only Hydroid Polyps resembling that Genus, which I have met in Australian waters." Lendenfeld may have seen the individuals of an earlier but unsuccessful invasion by this species, while Briggs was fortunate to observe the beginning of a second, successful establishment.

Australian Bryozoa received a great deal of attention during the nineteenth century by overseas workers such as Busk, Hincks, and Waters, and local specialists MacGillivray, Maplestone, Whitelegge, and Wooster, while more recently Bretnall, Livingstone, and Stach have made further contributions to their study. It is inconceivable that such distinctive and widely distributed species as those mentioned could have been overlooked by all. One can only conclude therefore, that the species in question were not present or certainly were not common, and that they have more probably become established during the past 20-30 years. Perhaps the strongest argument in favour of this hypothesis is the discontinuous, and in two cases extreme, localization in distribution.

The serpulid *Mercierella enigmatica* Fauvel is, as stated previously, a brackish-water form. It can withstand long periods in seawater of normal salinity but will not reproduce under those conditions. It is significant that when it was described as a new species (Fauvel 1922) the material came from Caen Canal, France, where it had never been seen before. Almost simultaneously it was discovered in London Docks by Monro (1924). Several years later it was found in Brittany, and then in quick succession it was reported from Spain, Tunis, the Black Sea, and California. Fauvel (1932), reporting its presence in India, wrote: "In the first description of *Mercierella* I wondered if it was not an exotic species brought on ships' bottoms to London and thence to Caen by the colliers plying between England and France. But what was its country of origin? The European fauna was so well known that it was not likely that such a common and thriving animal could have escaped detection . . . The discovery of *Mercierella* in the Ennur Backwater . . . solves the question. It must have been brought to London on ships' bottoms."

Fauvel seemed to be firmly convinced of that, and the species was in such abundance in the Madras area that this, it seemed, must be the region of origin. However, there seems to be no record of the fact that it was also abundant and thriving in Australian waters at that time. The author has certain knowledge of its occurrence, about 1932, as large madreporarian-like masses covering the shallows of a small tidal stream in the Sydney area. As it is so widely distributed in Australia, this continent and not India may have been the source of the specimens introduced to European waters. Whatever the country of origin there can be little doubt that ships have played an important role in extending the distribution of this species.

Another interesting serpulid, of much greater importance as a ship-fouling organism, in *Hydroides norvegica* Gunnerus. Under the name of *Eupomatus elegans,* it was described from Port Jackson as a new species by Haswell (1885), occurring rarely other than on certain seaweeds at a depth of 10-12 fm. Observations made by docking officers indicate that it was seldom, if ever, seen on ships fouled here 30 years ago, yet today it is the most important fouling organism in Port Jackson. Its rise in importance may be due to pollution of the harbour, or Haswell may have found it shortly after its introduction when it was still undergoing the process of establishment. Perhaps a combination of these and other factors would be nearer the truth, but in the absence of additional data one can only speculate. Another point in favour of its introduction is the fact that *Hydroides* is comparatively rare in Port Hacking and other inlets along this coast, while its distribution along the Queensland coast does not appear to be continuous; but it is certainly present to a greater or lesser degree in all the ports examined.

A serpulid, believed to be *H. norvegica,* has suddenly gained prominence as a fouler in New Zealand, where it was previously unknown. Authorities there consider it to have been introduced on ships in the trans-Tasman service, probably from Sydney. *Hydroides norvegica* is only moderately copper-tolerant but grows readily on the encrusting *Watersipora,* so that its development as a ship fouler in Australian waters may be related to the spread of this bryozoan.

The cirripedes are another important fouling group, for barnacles are rarely absent from a fouling community. In considering possible examples of introductions of members of this group, the widely publicized "export" of the Australian *Elminius modestus* Darwin is worthy of comment. In local waters this is an intertidal barnacle, occasionally living below this zone, sometimes as a fouling organism. Its range was wholly restricted to south-eastern Australia and New Zealand. In 1944 it was discovered (Bishop 1947) on test panels in Chichester Harbour, West Sussex, while the following year it was found attached to the bottoms of ships in the North Sea and North Atlantic service. Obviously it had become well established in British waters by that time. Two years later it was reported to have extended its range to Holland (Boschma 1948) and it appeared in France a little later. It has become a great pest on oyster and mussel beds in southern England and has spread from The Wash to Portland Bill and reached the Mersey. The first record of the presence of *Elminius modestus* in South African waters was made by Sandison (1950).

The distribution of barnacles by ships has already received attention from Bishop (1951), so that only points of Australian interest require comment. From examination of fouling material Bishop concluded that *Balanus improvisus* Darwin had become established in one of the southern Australian ports, but at present we have no evidence to confirm this. Bishop also wrote (1950) on the distribution of *Balanus amphitrite* var.

denticulata Broch. We have authentic specimens from a number of Queensland and Torres Strait localities, thus extending its known range into the Australian region. It occurs frequently on fouling plates from Townsville, Queensland.

Another interesting barnacle apparently added to the Australian fauna within recent years is *Balanus algicola* Pilsbry. It was originally described from South Africa, and this is the first record for the species outside that region. *B. algicola* was first noticed by Miss E. Pope towards the end of 1943, but was omitted from her paper on the barnacles of the Port Jackson area (Pope 1945) because of insufficient material for description and illustration. At this time it was rare, occasional specimens being found on the carapaces of crabs or on the tests of ascidians. During the course of marine fouling investigations it settled, sometimes in large numbers, on test panels, while in 1949 it was found for the first time directly attached to the antifouling paint surface on a small craft. Locally it has not yet assumed any importance as a fouler, although in South African waters it is probably the commonest fouling barnacle (Millard 1952).

The possibility that *Balanus algicola* is endemic cannot be overlooked. The ascidian *Pyura stolonifera* Heller, with which *B. algicola* is frequently associated on this coast, is also found in South Africa. The superficial similarity which this barnacle bears to *Balanus trigonus* may have led to its being considered by casual observers as the juvenile of the latter. Darwin (1854) recorded *Balanus tintinnabulum* Linn. from Sydney, but none of the varieties of this species are now known from this coast, while he seems to have mistaken *B. algicola* for juvenile *B. tintinnabulum.* It may therefore be that Darwin's record of the latter should have referred to *B. algicola.* On the other hand *Balanus algicola,* from the author's own observations, has considerably increased in numbers during the last 3-4 years and is fast becoming one of the commonest sublittoral barnacles on the open coast. Its present range extends from Eden to Port Stephens on the New South Wales coast.

So far the species dealt with have been sessile organisms, but possible transporation by ships is by no means restricted to this type of organism. Many years ago Chilton (1910) wrote an interesting note on the dispersal of crustacea by ships. Among other species he mentioned the presence of the European shore crab, *Carcinides maenas* Penn, in Victoria. Although doubted at first, its presence in Port Phillip was recorded by Fulton and Grant (1901). According to Miss E. Pope (personal communication), *Carcinides* now ranges from Westernport to Mallacoota, Vic. Well documented is the appearance of the Chinese crab *Eriocheir sinensis* Milne Edwards in western Europe. Hoestlandt (1945) gives a full account of the discovery of this species in Germany in 1912 and its subsequent spread over the Baltic region to Belgium and France. Again, ships offer the sole explanation for these translocations.

Even on the evidence submitted in this note there can no longer be any doubt that ships can and do play an important role in introducing marine invertebrates into new localities, often far from their point of origin. Statements such as that of Visscher (1938), "That there is no evidence of distribution of barnacles from one port to another by virtue of the attachment on bottoms of ships," are no longer tenable. If further evidence is required it is readily found in systematic literature. The alga *Asparagopsis armata* Harvey (Lucas 1947), the hydroids *Tubularia crocea* Agassiz (Browne 1899), *Clava leptostyla* Agassiz, *Obelia commissuralis* McCrady, and *Sertularia pumila* Linn. (Fraser 1938, p. 40), the serpulids *Hydroides norvegica* Gunnerus, *Mercierella enigmatica* Fauvel (Hartman 1952), and *Hydroides incrustans* (Monro 1938*a*), to name but a few, almost certainly have been distributed in this way.

General recognition of the shipping theory will have a bearing on some marine zoogeographical problems; it will allow some, but not necessarily all, anomalies in the distribution of shallow-water invertebrates to be attributed to this cause. It would also explain the well-nigh cosmopolitan range of many organisms. The bryozoans *Zoobotryon pellucides* Ehrenberg, *Bugula avicularia* Linné, *B. neritina* Linné, and *Conopeum reticulum* Linné, the polychaetes *Sabellastarte indica* Savigny, *Spirobranchus giganteus* Pallas, *Serpula vermicularis* Linné, and *Salmacina dysteri* Huxley, the ascidians *Ciona intestinalis* Linné and *Botryllus schlosseri* Pallas, and the algae *Enteromorpha intestinalis* Linné and *Ulva lactuca* Linné are some of the species whose ubiquity must be due in no small measure to the movements of shipping.

No doubt, in the days of sail, translocations were more easily made than at the present time, for voyages were long and slow and antifouling protection was poor. As a result organisms would have had little difficulty in settling on the wooden hulls which present a more favourable surface for settlement than does steel, and the sedate speeds of 5-6 kt would offer no great barrier to the survival of the organisms. Increased effectiveness in antifouling measures will reduce the possibility of further translocations, which in most instances are of no special economic importance. However, to prevent the entry of unwelcome migrants such as *Elminius modestus* Darwin and *Eriocheir sinensis* Milne Edwards, which have proved acute pests in another region, special measures may have to be devised.

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OSMOREGULATION IN AUSTRALIAN FRESHWATER MUSSELS (LAMELLIBRANCHIATA)

I. WATER AND CHLORIDE ION EXCHANGE IN HYRIDELLA AUSTRALIS (LAM.)

By I. D. Hiscock*

(*Manuscript received May* 26, 1953)

Summary

The chlorinities of the blood and pericardial fluid of *H. australis* are similar, but always exceed those of the normal external medium.

A study of blood chloride changes in mussels in media of different concentrations has shown that immediately following a change of medium there is a change in blood chlorinity, which tends to assume a new equilibrium level within 24 hr. The rapidity with which this change occurs depends upon the difference between the chlorinity of the blood and that of the external medium. A study of water exchange under identical conditions has shown that significant changes occur in the hydration of the mussel. In hypotonic media the mussel can regulate its water content; in hypertonic media it cannot, but its hydration assumes a new level within 24 hr. It is concluded that some part of the body surface is permeable to both salts and water.

The urine of the mussel is hypotonic to the blood; it remains remarkably stable in chlorinity despite changes in blood chlorinity. The role of the kidney as a regulating organ is discussed.

The significance of shell movements in osmoregulation is demonstrated. Shell closure has been shown to be an effective seal from the external medium, allowing the mussel to resist desiccation.

I. INTRODUCTION

In recent years research on osmotic relationships in aquatic animals has been concerned chiefly with: (1) finding the relationship between the concentration of the body fluids of the animals and that of their normal environment, (2) locating the organs responsible for regulating the concentration of the body fluids, and (3) correlating the effectiveness of the mechanisms with the needs of the animal in its normal habitat.

In freshwater mussels, these and related problems have been investigated chiefly by Philippson *et al.* (1910), Duval (1925), Ellis, Merrick, and Ellis (1931), Picken (1937), Florkin (1938), Krogh (1939), and Florkin and Duchateau (1948).

In the present work on *Hyridella australis* (Lam.) (=*Velesunio evansi* (Adams & Angas)) investigations are made on some aspects of these mechanisms. Only the chloride ion has been studied and it is realized that this does not give a complete picture of the mechanism of control.

II. METHODS

Specimens were collected from the Murray River at Mannum and Tailem Bend, S.A. After examination for cercaria they were placed in

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outdoor cement tanks (Hiscock 1950) until required. Water from these tanks was used in several experiments and is referred to as 'tank' water.

Blood was collected by ventricular puncture and centrifuged before analysis.

Chloride determinations were made by Van Slyke's (1923) method on samples of 0.5-1.0 ml. Twelve successive determinations of chloride on a standard NaCl solution showed that the method would determine to within 0.4mM chloride.

The depression of freezing point was determined with a Beckmann thermometer on 5-ml samples to within 0.005°C (based on 10 successive determinations with glass-distilled water).

Mussels were weighed using Florkin's method (1938). This method was made precise to 0.01 g by rolling the animals on a dry towel just before weighing.

III. Experimental Results

(a) *Depression of Freezing Point of the Blood of Normal Tank Specimens*

The Δ values of whole blood, converted to equivalent mM of NaCl (using data from International Critical Tables), ranged from 34.0 to 63.7mM, the mean for the six samples tested being 46.0mM with standard error 4.53mM. This compared with 25.5mM for *Anodonta cygnea* L. and 42.5mM for *Unio pictorum* (Lam.) (calculated from Δ values quoted by Dakin 1935).

(b) *Chlorinity of Blood, Pericardial Fluid, and External Media*

Blood chloride concentrations ranged from 10.0 to 25.6mM for 88 'tank' specimens, with a mean of 18.7mM and standard error of 0.37mM.

Table 1

CHLORINITY (mM) OF BLOOD, PERICARDIAL FLUID, AND EXTERNAL MEDIA

Medium	Blood		Pericardial Fluid	
	Mean	Standard Error	Mean	Standard Error
Murray River (1.3mM)	19.1	0.86	19.2	0.90
Outdoor tanks (3.38mM)	18.2	1.03	18.5	0.85
Indoor aquarium (12.8mM)	19.0	0.86	19.1	0.88

In *Anodonta cygnea* values as follows have been obtained: 17.1mM (Duval 1925), 9.85mM (De Waele 1930), 18.6mM (Ellis, Merrick, and Ellis 1931), 16.2mM (Picken 1937), and 8.45-14.1mM (Florkin and Duchateau 1948). Concurrent analyses of pericardial fluid showed that its chlorinity corresponded closely to that of the blood. The greatest difference observed was 1.8mM. Body fluid, obtained by cutting the foot and centrifuging the liquid so obtained, was found to be identical in chlorinity with the blood.

Chloride determinations were made on blood and pericardial fluid from mussels taken from three habitats of differing chlorinity, viz. lower Murray River, outdoor cement tanks, and a smaller indoor aquarium. The animals, originally from the Murray River, had lived in these surroundings for at least 6 months. The results, based on eight specimens in each case, are shown in Table 1. In no case do the values differ significantly, either between blood and pericardial fluid or between different samples of each.

(*c*) *Chloride Ion Exchange in Different External Media*

It has been shown fairly conclusively by Florkin (1938) that freshwater mussels are homoiosmotic in hypotonic media and poikilosmotic in hypertonic media. Florkin's evidence was based on freezing-point determinations of the blood of mussels kept in media of varying tonicity for 24 hr, after which they were believed to have reached equilibrium.

In section (*b*) above it has been shown that in different hypotonic media the blood chlorinity of *H. australis* did not vary significantly and was always above that of the external medium.

The *immediate* effect on the blood of a change in the external medium has been investigated briefly by Florkin and Duchateau (1948). They demonstrated a fall in blood chlorinity in *A. cygnea* after 6 hr in distilled water and a rise after 4½ hr in a medium containing 13.2mM of chloride. The rate of rise or fall in relation to the concentration of the medium and to time was not investigated.

To determine if such a relationship could be found in *H. australis*, a series of experiments was performed in which the mussels were placed in media of graded chlorinities and changes in blood chloride followed. The media were made up from NaCl and distilled water; none of the media interfered with the normal beat of ctenidial cilia in the mussels.

For the experiments, the animals were taken from the outdoor tanks and scrubbed under running water to remove epiphytic growth and mud. A small window, about 1.5 cm square, was cut in the left valve immediately lateral to the heart. At the commencement, a sample of blood, usually 0.5 ml, was withdrawn from the ventricle with a hypodermic syringe fitted with a 20-gauge needle, centrifuged, and its chlorinity determined. The shells were then propped apart with an 1/8-in. glass rod and the animals washed in the appropriate medium, then immersed in the medium in aquarium jars of about 1 l. capacity. Blood samples were taken on alternate hours for 5-6 hr and then at 24 hr. The total volume of blood removed never exceeded 3 ml. In every case the heartbeat of the mussels remained normal during the experiment.

Six different media were used and 12 mussels tested in each. Mean results are shown in Figure 1, where the blood chlorinity is expressed as a percentage of the original level.

It can be seen that there was an immediate response to a changed environmental concentration, the blood chloride increasing in high concentrations and decreasing in low. Within 6 hr the blood chlorinity had approached a new equilibrium level; by 24 hr the mussels in all media except the extremes had come into equilibrium. The calculated equilibrium values for mussels in each medium showed that the nearer the concentration of the external medium to that of the blood, the closer the two became at equilibrium.

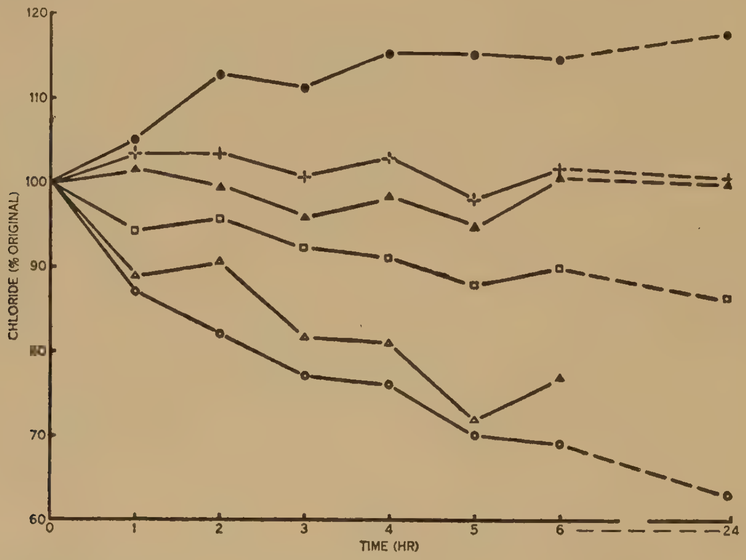

Fig. 1.—Effect of different media on blood chlorinity in *H. australis*.

○, Distilled water.
△, 5.6mM Cl⁻.
□, 10.0mM Cl⁻.
+, 14.1mM Cl⁻.
▲, 20.0mM Cl⁻.
●, 25.4mM Cl⁻.

(*d*) *Water Exchange in Different External Media*

Though the above results show definite changes in the blood chloride level following immersion in different external media, they give no indication as to whether the changes are due to movement of chloride ions across the body surface or to movement of water. The distinction can be effected by following weight changes in mussels in the media used previously.

Dakin and Edmonds (1931) pointed out that to appreciate the significance of weight changes in such experiments, it was necessary to determine the quantity of water present in the experimental animal at the commencement of the experiment. Accordingly a brief investigation was made of the hydration of the wet tissues of *H. australis*.

The mussels were scrubbed, drained, weighed, and then heated to constant weight at 90-100°C. Finally the shells were freed of dried tissues and weighed. The results are shown in Table 2; the percentage hydration is of wet tissues only, not total weight.

TABLE 2

HYDRATION OF WET TISSUES OF H. AUSTRALIS

Specimen No.	Total Wt. (g)	Shell Wt. (g)	Wet Tissue Wt. (g)	Dry Tissue Wt. (g)	Hydration (%)
103	42.99	13.71	29.28	1.91	93.4
104	39.26	12.80	26.46	1.105	95.8
105	38.27	12.56	25.71	1.15	95.4
106	44.03	13.03	31.00	1.58	94.9
107	43.89	15.28	28.61	1.83	93.5
108	31.15	14.41	16.74	1.35	91.8

For the present experiments 'tank' mussels were scrubbed and washed in the appropriate medium as in the previous experiments. Small "Perspex" wedges, similar in design to the aluminium ones used by Florkin (1938), were inserted between the shells at their ventral margins. The animals were weighed at the commencement of the experiment, immersed in the appropriate medium, then weighed hourly for 6 hr and at 24 hr. Twelve specimens were tested in each medium.

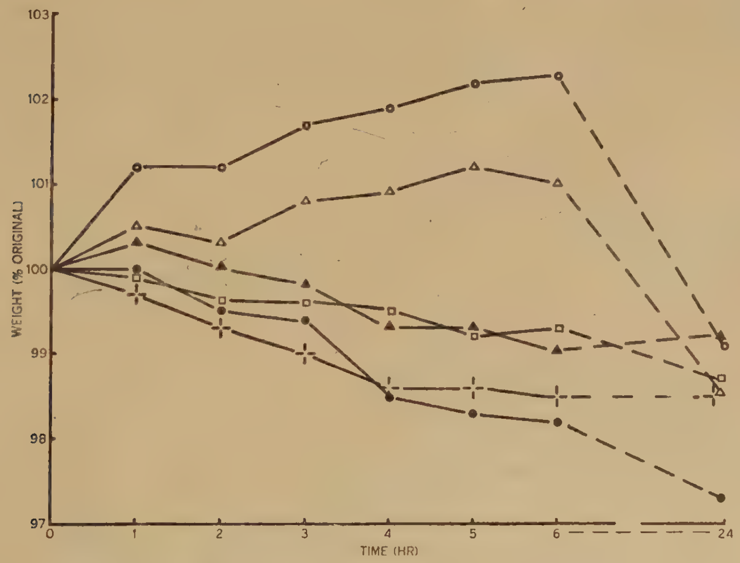

Fig. 2.—Weight changes in *H. australis* in different media.
○, Distilled water. +, 14.1mM Cl^-.
△, 5.6mM Cl^-. ▲, 20.0mM Cl^-.
□, 10.0mM Cl^-. ●, 25.4mM Cl^-.

The mean results are shown graphically in Figure 2. The weight is expressed as a percentage of that at the commencement of the experiment.

An analysis of variance on the weight variations, allowing for the initial weight of each animal by the method of covariance, showed that the mussels responded to the different media by a change in weight, the response being significant at the 0.1 per cent. level Mussels in media distinctly hypotonic to their blood showed weight regulation, while none of the others did. Where weight regulation had occurred, i.e. a resumption of normal hydration, the observed drop in blood chlorinity must have been due to chloride loss across some part of the body surface.

Simple calculations of blood chloride changes and water exchanges of mussels in hypertonic media showed that the amount of water exchanged was not sufficient to account for the observed changes in blood chlorinity. For example, a mussel with 40 g wet tissue weight at 94 per cent. hydration would contain 37.5 ml water. Allowing 10 ml 'bound' water, there would be 27.5 ml circulating fluid at a chlorinity of 18.7mM. On immersing the mussel in a medium with a chlorinity of 25mM, a drop in weight of 1.5 g could be expected in 24 hr. This would reduce the circulating volume to 26 ml and, assuming no chloride uptake, raise the chlorinity to 19.8mM, i.e. to 106 per cent. of the original. The observed rise under these conditions was to 117 per cent., so that chloride ions must have entered the body. Some part of the body wall of *H. australis* is therefore permeable to salts and to water.

(*e*) *Influence of Chemicals on Weight Regulation*

The effect of several chemical compounds, viz. ether, KCN, morphine sulphate, a barbiturate, and an analeptic, on weight regulation in *H. australis* was studied. The results are reported fully elsewhere (Hiscock 1953).

(*f*) *Role of the Kidney in Osmoregulation*

By vapour pressure measurements on blood and urine (removed from the nephridiopores) of *A. cygnea*, Picken (1937) showed that the urine originated as an ultra-filtrate of blood from the ventricle and became hypotonic to the blood during its passage through the nephridial tubes. This was confirmed later by Florkin (1938), using freezing-point determinations, and by Florkin and Duchateau (1948), using chloride determinations on 'liquide bojanien'. These several authors have further established that the kidney, apart from its excretory function, removes excess water entering the tissues osmotically, in the form of hypotonic urine.

The fluid used in the present experiments was taken from the bladder portions of the kidney, i.e. after its passage through the tubular or glandular portions of the organ. The fluid obtained was clear and colourless and was centrifuged before chlorinity determinations were made.

During the dissection to reveal the bladders, samples of blood and pericardial fluid were also obtained. The chlorinities of these three fluids taken from six mussels are shown in Table 3.

TABLE 3*

CHLORINITY (mM) OF BLOOD, PERICARDIAL FLUID, AND URINE IN H. AUSTRALIS

Specimen No.	Blood	Pericardial Fluid	Urine
235	15.2	14.4	2.19(?)
236	10.0	10.0	7.32
237	14.4	14.0	8.00
238	16.0	16.0	9.18
239	19.0	19.0	16.0
240	21.9	21.8	14.0

* The extreme range in blood chlorinity of the specimens in Table 3 was exceptional for a small sample and should not be regarded as typical.

These results show that the urine of *H. australis* is hypotonic to the blood. Mean values show that its chlorinity is 60 per cent. of that of the blood, compared with 60 per cent. (Picken 1937) and 55 per cent. (Florkin and Duchateau 1948) for *A. cygnea*.

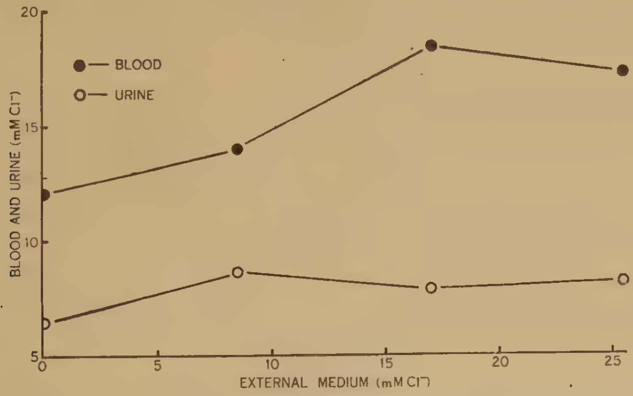

Fig. 3.—Relation of blood and urine following induced changes in blood chloride (chloride expressed as mM).

In an attempt to determine how efficiently the kidney could act as a regulator of salt and water balance, a series of groups of six mussels was set up, each group being immersed in a different external medium (ranging from 0 to 25.6mM Cl^-) for 24 hr with their shells propped apart. Under slightly different conditions, where holes were cut in the shells as well as the valves being propped open with wedges, blood chlorinity changes were observed (Fig. 1). These changes would alter the pericardial fluid entering the kidney.

Chloride determinations were made on the blood and urine of each animal following this treatment. The results are shown in Figure 3. The points plotted in Figure 3 are the means of the six animals used in each case. Table 4 shows these means and their standard errors. The change in blood chlorinity due to a changed external medium was significant at the 0.1 per cent. level; the variation in urine chlorinity was not significant at the 5 per cent. level.

TABLE 4

BLOOD AND URINE CHLORINITIES (mM) OF GROUPS OF SIX MUSSELS AFTER 24 HR IN DIFFERENT MEDIA

Medium (mM Cl⁻)	Blood		Urine	
	Mean	Standard Error	Mean	Standard Error
0	12.04	0.89	6.41	0.51
8.5	14.06	0.73	8.58	0.49
17.0	18.46	0.44	7.86	1.14
25.5	17.41	0.68	8.21	0.35

These data demonstrate that the urine is always hypotonic to the blood; in fact as the blood chloride rises the urine becomes more hypotonic, the kidney removing a greater percentage of chloride from the pericardial fluid. The fact that the urine remains stable in chlorinity suggests that the kidney functions to some extent independently of the external medium.

(*g*) *Significance of Shell Movements in Osmoregulation*

To prevent the intervention of shell movements as a possible factor in the above experiments, the shells were kept apart either with "Perspex" wedges or thin glass rods. To determine whether shell movements were effective in controlling water balance, two sets of 12 mussels were scrubbed and rinsed in distilled water. One set unwedged and the other wedged were placed in distilled water and each mussel weighed hourly for 6 hr and at 24 hr. The hourly means for each set are shown in Figure 4, and with their standard errors in Table 5.

It is clearly seen that though the wedged specimens showed weight regulation after 24 hr, they took up water for at least 6 hr. The unwedged animals, on the other hand, showed no significant change in weight during the 24 hr, this indicating that with the shells left to function normally water balance is maintained. The small weight variations noted were due probably to varying quantities of urine in the bladder at the time of weighing.

It has been reported (Hiscock 1950) that a small specimen of *H. australis* had been found to have resisted desiccation for at least 3 months at 22°C by keeping its shells tightly closed. The following experiment was carried out to investigate further the resistance to desiccation.

An aquarium dish, with about 4 in. of Murray River mud covered by 2 in. of river water and containing six mussels, was left to dry during the hotter part of the summer of 1950-51. Within 2 wk only moist, hard mud remained with five of the animals buried in it, one mussel having died.

TABLE 5

OSMOREGULATION BY MUSSELS IMMERSED IN DISTILLED WATER

Hours from Commencement	Wedged Specimens		Unwedged Specimens	
	Mean Wt. (%)	S.E.	Mean Wt. (%)	S.E.
0	100	—	100	—
1	101.2	0.25	99.8	0.11
2	101.2	0.39	99.8	0.15
3	101.7	0.52	99.6	0.15
4	101.9	0.55	99.5	0.16
5	102.2	0.54	99.5	0.17
6	102.3	0.57	99.6	0.20
24	99.1	0.54	99.8	0.23

After 3 months the mud had dried completely and set hard. The five mussels were retrieved by cracking the mud; one was dead. Of the four remaining, the blood chlorinity of two was determined immediately; the other two were weighed and immersed in 'tank' water until constant weight was attained. Their blood chlorinity was then determined.

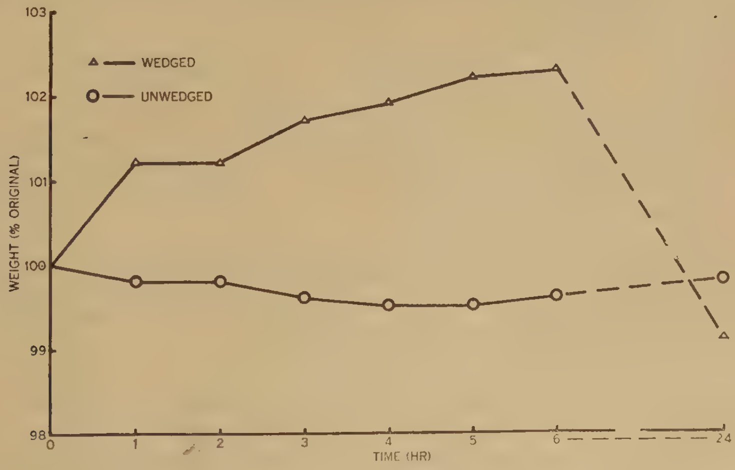

Fig. 4.—Effect of wedging on water balance in *H. australis* (mussels immersed in distilled water).

The results for the individual mussels were:

Specimen 353: Valves completely sealed, muscle tone good, tissues well hydrated. Blood chlorinity 33.5mM Cl^-, i.e. 80 per cent. above the mean for untreated mussels.

Specimen 354: As above, blood chlorinity 27.2mM Cl^- (45 per cent. above normal).

Specimen 355: Valves sealed. Original weight 13.46 g, rising to a constant 15.30 g in 5 hr, i.e. a rise of 13.6 per cent. Final blood chlorinity 21.3mM.

Specimen 366: Valves sealed. Original weight 28.22 g, rising to a constant 31.26 g in 5 hr, i.e. a rise of 10.8 per cent. Final blood chlorinity 22.6mM.

These results show that *H. australis* can withstand desiccation for at least 3 months, undergoing partial dehydration and tolerating a rise in blood chlorinity to 180 per cent. of normal.

Within 5 hr of returning to water both hydration and blood chlorinity approached levels found in untreated animals.

IV. Discussion

It is now generally accepted that the origin and maintenance of osmotic independence in freshwater invertebrates is the resultant of a complex series of phenomena including the active absorption of ions from the external medium, the low permeability of the body surface to salts and to water, and the function of the excretory organs.

Active absorption of ions has been demonstrated in freshwater molluscs, including *Anodonta* and *Unio pictorum* L., by Krogh (1939). It is proposed to commence similar work on *H. australis* in the future.

It can now be confirmed that the other components of the regulatory system, as well as several components not previously recorded from freshwater mussels, viz. the power of weight regulation and the influence of shell movements, all contribute to the maintenance of osmotic independence.

The bulk of evidence in the literature suggests that in external media of concentration lower than the normal internal medium, freshwater mussels are homoiosmotic. In the present work, while total osmotic pressures were not determined, the chlorinity concentrations did in fact show a remarkable constancy when the mussels had been given prolonged immersion in dilute media (see Table 1).

In more concentrated media Florkin (1938) has proved that *A. cygnea* becomes poikilosmotic. Though the present work does not include comparable data for these media, the observed changes in weight and blood chlorinity suggest a similar state of affairs.

Following sudden immersion in media differing in chlorinity from its blood *H. australis* shows an immediate change both in blood chlorinity and weight (Section III (*c*) and (*d*)). The rate of gain or loss of both chloride and water is dependent on the difference between blood and external medium (see Hiscock 1953, Fig. 3).

Within 24 hr the blood chlorinity reaches or closely approaches a state of equilibrium in mussels in media both hypotonic and hypertonic to their blood. The blood chlorinity at equilibrium in media at the extremes of chlorinity is always different from that of the medium. The mussel evidently has the power to control, if not regulate, its blood chlorinity.

Weight changes differ markedly from chloride changes in distinctly hypotonic media. Following an initial weight increase, volume regulation occurs. There is no comparable process in hypertonic media. Similar results have been obtained in earthworms and a turbellarian (Adolph and Adolph 1926), in *Nereis* sp. (Ellis 1937), in *Pagurus longicarpus* Say (Maloeuf 1938), and a soil nematode (Stephenson 1942).

The present results confirm in general Florkin's (1938) findings for *A. cygnea* but differ in one or two significant aspects, e.g. in showing an initial weight increase in distinctly hypotonic media. The volume regulation in operation brings the weight to a nearly normal level again so that at equilibrium no apparent change has occurred. The absence of a chloride-regulating mechanism to restore to the blood chloride ions lost in hypotonic media suggests that some compensatory factor must operate to maintain the homoiosmoticity observed by Florkin (1938). The nature of this factor is not known.

If the shells of *H. australis* are wedged apart an initial increase in weight follows, even when the mussel is immersed in its normal medium. With the shells closed no such increase occurs, even in distilled water (Fig. 4). This suggests that the closed shells are an effective seal from the external medium and are impermeable. Impermeability of the integument has been noted also in the freshwater crustaceans *Potamobius astacus* L. (Huf 1936) and *Cambarus bartoni* Fabr. (Maloeuf 1937). In freshwater mussels, apart from converting the body from a naked state, shell closure and shell impermeability are of prime importance in drought resistance in the natural habitat of many Australian species. Large numbers of *H. australis* were collected in March 1951 from the Crawford River, Victoria, from drying black mud, and the mortality rate was less than 5 per cent.

Shell closure is accompanied by a decrease in respiration (Hiscock 1953) and in heartbeat rate (Koch 1917). The former is a logical result of the cessation of water movement but the significance of the latter merits discussion. Shell movements result in the displacement of large volumes of blood in the sinuses and are of great importance in blood circulation. Urine formation requires both heartbeat and an osmotic stream of water into the body. As long as heartbeat continues urine will be produced, and as long as water enters the body urine must be produced to maintain a normal water balance. When the shells are apart water enters the body osmotically, the heart beats, and the flow of urine removes the excess water. When the shells close water no longer enters osmotically, and a constant flow of urine need not be produced especially to remove this excess water. In fact it must not be produced if water balance is to be maintained. The simplest means of reducing urinary flow is a reduction of heartbeat, which occurs under these conditions.

Normally the kidney produces a urine hypotonic to the blood. If the organ were really efficient as an osmoregulator, it would be expected to produce a urine of higher chlorinity in animals in hypertonic media than that normally produced (mussels have been collected from ponds with a chlorinity greater than 20mM). The data above show, however, that the urine is constant in chlorinity, indicating an independent function of the kidney. This point is being investigated further.

V. ACKNOWLEDGMENTS

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OSMOREGULATION IN AUSTRALIAN FRESHWATER MUSSELS (LAMELLIBRANCHIATA)

II. RESPIRATION AND ITS RELATION TO OSMOREGULATION IN HYRIDELLA AUSTRALIS (LAM.)

By I. D. HISCOCK*

(*Manuscript received May* 26, 1953)

Summary

The oxygen consumption of *H. australis* when the shells are open is thrice that when they are closed.

As the chlorinity of the external medium rises, in the range 0-25.5mM chloride, oxygen consumption diminishes, indicating a lower energy production. Ether inhibits slightly the process of weight regulation in the mussel. With intact animals KCN has no observed effect either on this process or on respiration; under different conditions KCN inhibits respiration and ciliary activity of isolated gills. A barbiturate and an opiate both inhibit weight regulation to a slight degree and reduce oxygen consumption; neither affects ciliary activity. An analeptic reverses the effect of the opiate, increases respiration, and is without effect on cilia.

The probable relationship between osmoregulation and respiration, and the influence of the nervous system upon both are discussed.

I. INTRODUCTION

There is strong evidence to support the hypothesis relating oxygen consumption to osmoregulation (Schlieper 1930, 1935). Raffy and Fontaine (1930), Beadle (1931), Bouxin (1931), Fox and Simmonds (1933), Löwenstein (1935), Maloeuf (1937), Hopkins (1949), and Flemister and Flemister (1951), among others, have data which lend strong support.

The literature reveals few data on respiration in freshwater mussels. Weinland (1919) showed that oxygen consumption in *Anodonta cygnea* L. diminished under starvation conditions and Gartkiewicz (1922) showed that *Anodonta* existed in one of two states, 'active' or 'sleep', with oxygen consumptions related in the ratio of 3 : 2 respectively.

In a previous paper (Hiscock 1953), it was shown that the freshwater mussel *Hyridella australis* (Lam.) regulated its water content and chloride exchange in media hypotonic to its blood.

In the present work the following were studied:

(1) Normal respiration in the mussel;
(2) The relationship of respiration to osmoregulation; and
(3) The possible pathways of control of the osmoregulatory and respiratory mechanisms.

The mussel used in all experiments was *Hyridella australis* (Lam.) (= *Velesunio evansi* (Adams & Angas)).

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II. METHODS

Oxygen consumption in *H. australis* was determined by the 'open' method of Galtsoff and Whipple (1930). Four aquarium jars were bound together on sheet cork and covered by a wooden frame bearing four stirring rods running at 5-10 r.p.s. At the commencement of each experiment, 1 l. of fluid was run into each jar and vigorously aerated for 2 min, a mussel placed in each jar, and a 3-cm layer of heavy liquid paraffin layered on the fluid surface.

Unless otherwise stated, all mussels were previously kept in 'tank' water at 20°C for at least 48 hr and were scrubbed and wedged before placing in the apparatus. The wedges, made of "Perspex" in a design similar to those used by Florkin (1938), were inserted between the shells at their ventral margins.

Water samples of approximately 1.5 ml were withdrawn and oxygen determinations made by the method of Fox and Wingfield (1938). Samples were taken hourly for 6 hr and results expressed as ml at N.T.P. per 100 g wet tissue per hr. This method gave a precision of 2 per cent., as shown by repeated trial.

The water used in most experiments was 'tank' water (Hiscock 1953) filtered through two thicknesses of Whatman No. 1 paper. It was realized that bacteria might be present in the water but over the period of 6 hr the consumption of oxygen due to bacteria was so small as not to influence the determinations made.

All experiments were carried out at 20 ± 1°C in a constant-temperature room. Mussels were weighed by Florkin's (1938) method to 0.01 g (see Hiscock 1953).

TABLE 1

OXYGEN CONSUMPTION (ML AT N.T.P.) OF H. AUSTRALIS UNDER NORMAL CONDITIONS

Specimen No.	Total Wt. (g)	O_2/100 g Wet Tissue/Hr	Comments
1	42.15	0.624	Open part of time
2	38.06	0.905	Open all the time
3	45.72	0.781	Open all the time
4	37.58	0.351	Shut all the time
5	70.45	0.366	Shut most of time
6	69.95	0.794	Open part of time
7	39.75	0.640	Open part of time
8	53.95	1.099	Open all the time

III. RESULTS

(a) *Normal Respiration*

Eight mussels were tested unwedged. Since it was impracticable to record shell movements concurrently, the animals were observed at frequent intervals and the positions of their shells and their behaviour noted (Table 1).

The figures quoted in Table 1 give only the mean consumption per hour for 6 hr. The complete hourly analysis with shell movements taken into account is not included; only the average consumption with shells open or closed respectively is given.

Mussels with shells closed consumed an average of 0.396 ml/O_2/100 g wet tissue/hr (standard error of mean for 22 observations 0.045 ml); opening or movement of the shells increased the consumption to 1.027 ml/hr (standard error of mean for 24 observations 0.057 ml), i.e. to thrice that of the shell-closed state.

These figures are similar to those of Gartkiewicz (1922) for *Anodonta*. They show that shell closure reduces body activity; Koch (1917) showed that reduced heartbeat rate is a further result.

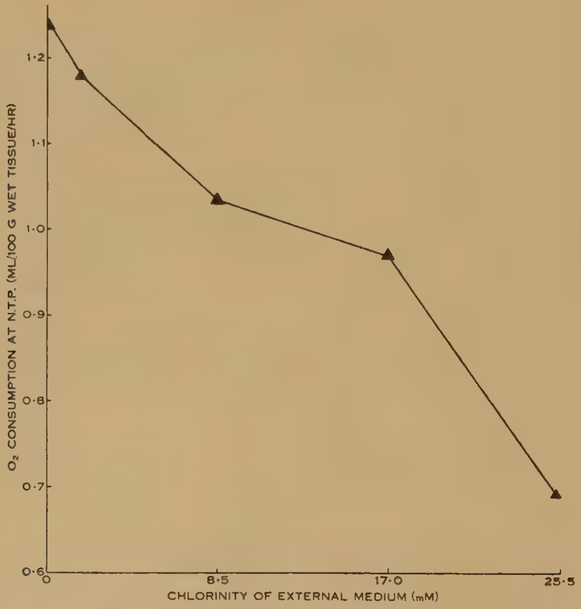

Fig. 1.—Effect of the external medium on oxygen consumption in *H. australis*.

(*b*) *Effect of the External Medium on Respiration*

Oxygen consumption of sets of eight wedged mussels immersed in different media was measured. The media were made up from NaCl and distilled water and ranged in chlorinity from 0 to 25.5mM Cl^-.

The mean values for oxygen consumption in different media are graphed in Figure 1 and are given with their standard errors in Table 2.

Figure 1 indicates that oxygen consumption in the mussel is partly under the influence of the concentration of the external medium. An analysis of variance, conducted on the rate of consumption of oxygen/100 g wet tissue/hr, allowing for the weight of wet tissue in each animal, showed that the concentration of the external medium had a significant effect on respiration. As the external chlorinity rose, the oxygen consumption decreased, the decrease being significant at the 0.1 per cent. level.

TABLE 2

MEAN OXYGEN CONSUMPTIONS (ML AT N.T.P.) FOR SETS OF EIGHT MUSSELS IN DIFFERENT MEDIA

Medium	O_2 Consumption/100 g Wet Tissue/Hr	
	Mean	Standard Error
Distilled water	1.24	0.016
'Tank' water	1.18	0.034
8.5mM Cl^-	1.03	0.050
17.0mM Cl^-	0.97	0.022
25.5mM Cl^-	0.69	0.022

(c) *Effect of Chemical Compounds on the Mussel*

(i) *Water Exchange*

It was shown in a previous paper (Hiscock 1953) that *H. australis* regulated its water exchange in media hypotonic to its blood. To investigate the possible pathways of control of this regulation, experiments were performed with substances as follows:

(1) *Ether*.—Six mussels, scrubbed and wedged, were immersed in 'tank' water containing 10 g ether per litre and weighed hourly for 6 hr. The animals were then washed, transferred to fresh 'tank' water, and weighed after 24 hr. The results are graphed in Figure 2.

The quantity of ether added was the same as Florkin and Duchateau (1948) used. It was realized that the concentration would probably decrease during the 6-hr period, but the residual quantity was quite sufficient to maintain anaesthesia.

Within 1 hr of immersion all specimens were anaesthetized. They showed loss of tonicity of the adductor muscles (causing shell gape) and loss of sensitivity of the siphons and foot, the latter protruding through the shell aperture and showing no response to mechanical or mild faradic stimulation. This state of anaesthesia was maintained for 6 hr in etherized water, during which time the mussels showed a marked increase in weight. Replacement in fresh water was followed by gradual recovery and weight regulation, a normal balance being restored at the end of 24 hr. The results confirmed Florkin and Duchateau's (1948) findings for *A. cygnea* in every way.

(2) *KCN*.—Six specimens were prepared and each received an injection of KCN into the foot, at a dosage of 1 ml of 0.01 per cent. KCN (in 0.1 per cent. NaCl) per 100 g total weight. Each mussel was weighed immediately, then hourly for 6 hr and after 24 hr, being immersed in 'tank' water during that time.

The results (Fig. 2) show that no appreciable weight variations occurred during the first 6 hr. Normal regulation was apparent at the end of 24 hr.

Consequently, injections of more concentrated solutions of KCN, viz. 0.1 and 1 per cent., were tried on several mussels. Again no response was evoked. It had been assumed by Florkin and Duchateau (1948) that an injection into the foot of a mussel penetrated to the blood and other tissues. Since the point assumed importance with the unexpected insensitivity to cyanide, the following experiment was performed for confirmation. Several mussels received an injection of 0.1 per cent. KCN into the foot and blood samples were tested for the presence of cyanide after 2 hr by the method outlined in Partington (1921). The CN is converted to ferrocyanide with

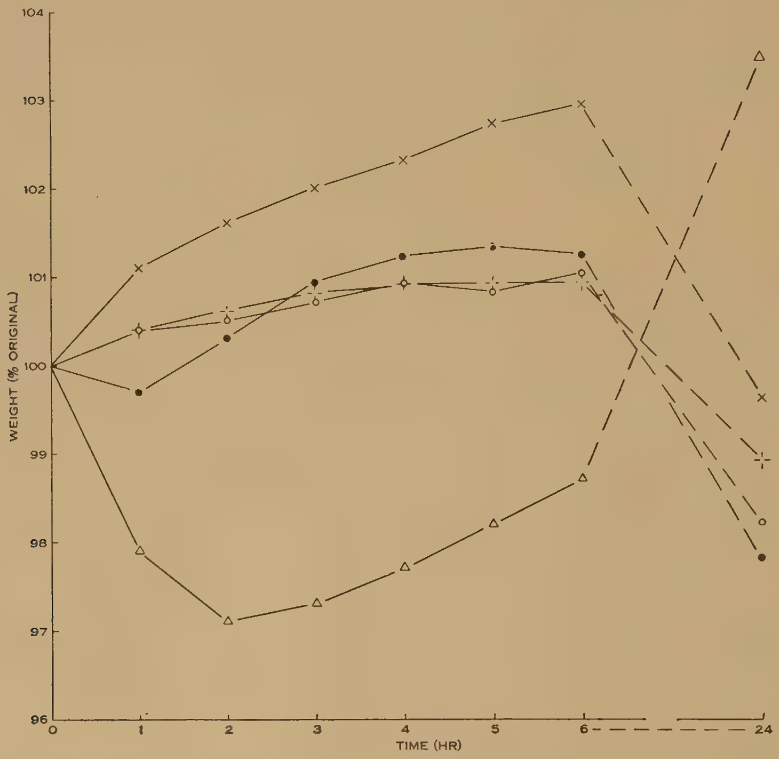

Fig. 2.—Effect of various compounds on water balance in *H. australis*.

○, Control ('tank' water).
×, Ether.
+, KCN.
△, "Evipan Sodium."
●, Morphine sulphate.

ferrous hydroxide and, in the presence of a ferric salt, prussian blue is formed, giving a bluish green colour. The method will detect one part HCN in 50,000 of water.

Cyanide in small quantity was detected in each case. KCN, under these conditions, has no effect on weight regulation in *H. australis*.

(3) *"Evipan Sodium"* (*Sodium N-methylcyclohexenylmethylbarbiturate*).—Twelve mussels were prepared as before and each received an injection of the drug at a dosage of 1 ml of a 10 per cent. aqueous solution per 100 g total weight, the same dosage as used by Florkin and Duchateau (1948). Weighings were carried out hourly for 6 hr and at 24 hr; the results are shown in Figure 2.

The immediate visible effect of the drug was to bring about a marked and localized contraction of the foot at the site of injection. This persisted for 6 hr but had largely subsided at the end of 24 hr. None of the animals appeared completely narcotized but all were sluggish for several days. The preliminary loss of weight was followed by a marked increase as the local action of the drug subsided. The weight-regulating mechanism was markedly inhibited.

(4) *Morphine Sulphate*.—Preliminary investigation showed that at least 50 mg of morphine sulphate per 100 g total weight of mussel were required to produce anaesthesia. In the experiment proper, 12 mussels were prepared and each received an injection of an aqueous solution of morphine sulphate at the above dosage. Weighings were carried out hourly for 6 hr and at 24 hr. The results are graphed in Figure 2.

The immediate effect of the compound was similar to that of the barbiturate, i.e. a marked muscular response near the site of injection accompanied by a slight decrease in weight and followed by weight increase, then regulation. All animals had recovered within 24 hr. The effect of morphine sulphate on the mussel is milder and of shorter duration than that of the barbiturate.

(5) *Effect of an Analeptic, Pyridine β-carboxylic Acid Diethylamide, on Normal and Morphinized Mussels*.—If the effect of morphine sulphate were due to inhibition of nervous activity, leading to respiratory inhibition; or to a direct action on respiratory mechanisms, it was felt that an analeptic such as pyridine β-carboxylic acid diethylamide might reverse the effect.

Accordingly, six mussels were prepared; four received 50 mg morphine sulphate per 100 g total weight. Of these, two received a further injection of the analeptic after 3½ hr, allowing 150 mg per 100 g total weight. One mussel received the analeptic alone at the same dosage at the same time; the control animal received 0.1 per cent NaCl. Weighings were carried out as before and results are shown in Table 3.

The analeptic preparation was CIBA "Coramine", containing 250 mg/ml pyridine β-carboxylic acid diethylamide.

The two mussels receiving morphine sulphate alone behaved as in the previous experiment. Those receiving "Coramine" while anaesthetized showed a rapid return to normal and lost water. Those receiving "Coramine" alone or NaCl showed no significant change in weight.

TABLE 3

EFFECT OF "CORAMINE" ON THE WATER EXCHANGE OF NORMAL AND MORPHINIZED MUSSELS

Specimen No.	Total Wt. (g)	Drug	Weight (% of original) After							
			0	1	2	3	4	5	6	24 Hr
229	107.62	Morphine sulphate	100	99.8	100.6	101.1	101.1	101.3	101.7	97.0
230	68.46	Morphine sulphate	100	99.6	100.0	100.8	101.3	101.3	101.1	98.7
231	69.26	Morphine sulphate + "Coramine"	100	100.8	101.1	101.3	98.4	97.8	95.6	96.5
232	106.64	Morphine sulphate + "Coramine"	100	100.8	101.3	101.7	95.5	93.3	91.3	96.7
233	80.37	"Coramine" only	100	100.4	100.5	100.8	100.9	100.7	100.2	101.5
234	65.72	NaCl	100	100.2	100.3	100.2	100.3	100.3	100.3	99.0

It is concluded that the mechanisms regulating water exchange are, in part at least, dependent on respiration and are probably under nervous control.

TABLE 4

EFFECT OF CHEMICAL COMPOUNDS ON RESPIRATION IN H. AUSTRALIS

Compound	No. of Specimens	O_2 Consumption (ml at N.T.P.)		Percentage of Control
		Mean	S.E.	
Control	8	1.28	0.036	—
KCN	4	1.24	0.153	96.8
Barbiturate	8	0.47	0.034	36.7
Morphine sulphate	8	0.61	0.044	47.7
"Coramine"	8	1.21	0.138	94.5

(ii) *Respiration*

The effects of the chemical substances noted above may have been due partly to their effect on respiration. The following experiments investigated this possibility.

The experimental procedure for measuring oxygen uptake and the dosage and administration of the substances were as described above. The mean oxygen consumption over 6 hr was determined and is expressed as ml/100 g wet tissue/hr. The results, with their standard errors, are assembled in Table 4.

The results are in keeping with those for weight regulation, i.e. marked inhibition by "Evipan," less marked by morphine sulphate, and no significant effect by KCN. Results with "Coramine" differed from the others in that the respiratory rate rose steeply above normal during the first 2 hr, then slowly descended to a slightly subnormal level. This is illustrated in Table 5.

TABLE 5

EFFECT OF "CORAMINE" ON RESPIRATION IN H. AUSTRALIS

Time (hr)	O_2 Consumption/100 g Wet Tissue/Hr (ml at N.T.P.)
1	1.218
2	1.491
3	1.356
4	1.182
5	0.919
6	0.826

(iii) *Ciliary Activity*

It was conceivable that the changed respiratory rates noted above were due to the chemicals acting on the ctenidial and mantle cilia causing a greater or lesser flow of water over these organs. A purely qualitative investigation was made to check this possibility. Small pieces of gill lamina were placed in tap water with the chemical added to the water and the frontero-lateral cilia of the filaments examined under a high-power microscope at hourly intervals. The results are shown in Table 6.

TABLE 6

EFFECT OF CHEMICALS ON CILIARY BEAT IN H. AUSTRALIS

N = normal, F = feeble, C = ceased

Drug	Concentration (%)	Ciliary Beat After							
		0	1	2	3	4	5	6	24 Hr
KCN	0.01	N	F	C	C	C	C	C	C
"Evipan"	5	N	N	N	N	N	N	N	C
Morphine sulphate	1	N	N	N	N	N	N	N	C
"Coramine"	5	N	N	N	N	N	N	N	C
Control (tap-water)		N	N	N	N	N	N	N	N

The results show clearly that respiratory inhibition was not due to ciliary failure. In the one case where ciliary beat was affected, viz. with KCN, respiration was normal.

(iv) *Effect of KCN on the Respiration of Isolated Gill Tissue*

The insensitivity of the intact animal but the sensitivity of gill cilia to cyanide was further investigated by determining the effect of cyanide on gill tissue respiration, using the Warburg technique.

Two separated gill laminae were bisected and the four pieces placed in 3.0 ml phosphate buffer (40mM and pH 8) in a Warburg flask. The centre cups contained 0.4 ml of 0.5M KOH, with filter paper, and KCN was introduced by Robbie's (1946) method to produce a concentration of 0.2mM in the buffer. The flasks were agitated at 50 c/min at 26°C for 1 hr. The gill pieces were recovered, pressed gently between filter paper, and weighed.

In buffer alone, the Q_{O_2} was 231 cu. mm/g wet tissue/hr (mean of five tests, standard error 6.14 cu. mm). In buffer plus CN, the Q_{O_2} was 98 cu. mm/g wet tissue/hr (mean of four tests, standard error 2.46 cu. mm). Therefore 0.2mM KCN produced 67 per cent. inhibition of oxygen uptake.

IV. DISCUSSION

Respiration in freshwater mussels is essentially a process of gaseous exchange across the ctenidial and mantle walls and requires a stream of water. A reduction of water flow would be expected to reduce respiratory rate. This reduction of flow can result from either closing or partial closing of the shells or reduced ciliary beat. It is not surprising to find that shell closure results in considerable reduction of oxygen uptake. This was also noted in *Anodonta* by Gartkiewicz (1922).

During shell closure the mussel continues respiration at a slow rate. Cole (1926) has demonstrated that *Anodontoides ferrussacianus* Lea could live for several days in the absence of available oxygen, producing carbon dioxide during that time. It was shown by the present author (Hiscock 1950) that prolonged shell closure is a common feature of mussels under normal conditions and that it is an important factor in osmoregulation (Hiscock 1953).

In media hypertonic to the blood, where neither weight nor chloride regulation takes place, the oxygen consumption remains low. It is here that the mussel differs from marine animals. In euryhaline marine species oxygen consumption is at its lowest when the external medium is isotonic and rises as the latter becomes hypo- or hypertonic to the blood. This relationship is fully discussed by Schlieper (1930, 1935).

It remains to show whether an induced decrease in respiration is related to inhibition of osmoregulatory mechanisms and, if so, how the decrease is brought about.

Weight regulation was inhibited by ether, but whether the effect was a direct one or due to an increase in the permeability of the cell membrane (see Heilbrunn 1943, p. 143) is not known. Sodium N-methylcyclohexenylmethylbarbiturate and morphine sulphate both inhibited weight regulation, the former to a greater extent. The immediate effect of both substances was masked to a large extent by the intense tissue reaction at the site of injection. Dakin and Edmonds (1931) have pointed out that muscular contraction resulting from unfavourable conditions such as these may cause expulsion of water with consequent loss of volume and weight, and hence obscure the actual effect of the agent causing the contraction. It is of interest that Florkin and Duchateau (1948), using the same dose of the barbiturate on *A. cygnea,* recorded no such tissue reaction but only gradual narcosis followed by recovery after an unstated period of time. Neither compound affected ciliary activity for at least 6 hr, yet both reduced oxygen consumption.

It is difficult to correlate the known effects of the above substances in mammals with the present data. "Evipan" brings about central depression by its action on the cerebral cortex (Sollmann 1948) and morphine sulphate acts both on the respiratory centre and cortical and subcortical centres of the brain (Bastedo 1947). It is probable that in freshwater mussels both drugs act through nervous pathways to the respiratory mechanisms, and thus to the regulating mechanism itself. The effect of the analeptic "Coramine" lends support to this. Here a respiratory stimulant can reverse the effect of a respiratory inhibitor which is also inhibiting the weight-regulating mechanism.

The insensitivity of the whole mussel and the sensitivity of the isolated gill laminae to cyanide is of great interest. Beadle (1931) showed that water balance and respiration in *Nereis diversicolor* Müller were affected by cyanide; Solandt *et al.* (1934) and Chapeau (1932) have demonstrated respiratory inhibition by KCN in marine mussels. Hopkins (1949) showed that cyanide produced moderate inhibition of respiration of clam gills only during autumn. The problem will be investigated further in *H. australis.*

The picture of osmoregulation in freshwater mussels is by no means clear. The present data show that movements of chloride ion and water between the mussel and its environment are determined largely by the relative concentrations. Further, oxygen consumption, hence energy production, decreases with rising external chlorinity. The interrelation of movements of chloride ion and water with oxygen consumption are shown in Figure 3, the data for which are drawn from Hiscock (1953) and the present paper.

In its normal environment, i.e. one markedly hypotonic to its blood, closing of the shells relieves the mussel from osmotic embarrassment. When the shells open, chloride ions are lost; from the data of Krogh (1939) it must be assumed that these are replaced by active absorption from the environment.

Under the same conditions the uptake of water is regulated, probably by the activity of the kidney. Both processes must require energy and it has been shown that a supply of oxygen to make this available is forthcoming under these conditions.

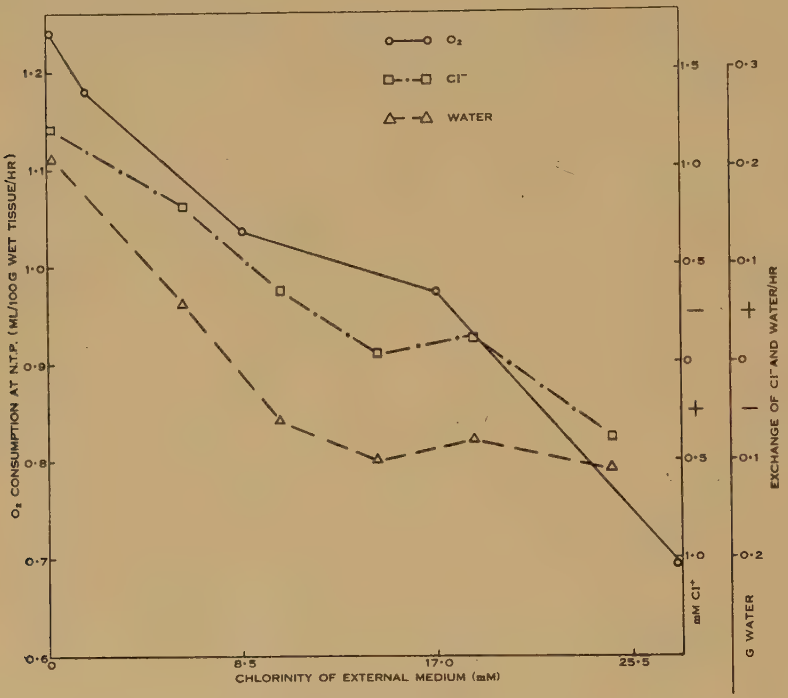

Fig. 3.—Water and chloride ion exchange and respiration in *H. australis* in relation to concentration of the external medium.

The present data also suggest a possible scheme of pathways of control of osmoregulation. The scheme is pictured as follows:

Stimulation
(tonicity of medium)
↓
Chemoreceptors (?)
↓
Nervous system
↓ ↓
Respiration................(Energy production)...............Osmoregulation.

Further experimental work will help elucidate the true state of affairs.

V. ACKNOWLEDGMENTS

The author wishes to express his indebtedness to Mr. I. M. Thomas of the University of Adelaide for frequent advice, to the Commonwealth Research Grant of the Universities of Adelaide and Queensland, to his wife for assistance in the mathematical calculations, and to Professor W. Stephenson for suggestions in the preparation of the paper.

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A SURVEY OF THE WESTERN COASTAL DUNE LAKES OF THE NORTH ISLAND, NEW ZEALAND

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Summary

A biological survey of 26 lakes of the western dune series of the North Island was made during the summers of 1949 and 1950. At each lake a shore-line and bathymetric survey was made and contour maps have been prepared. Temperature and transparency measurements were also taken. Analysis for essential chemicals, particularly oxygen, was made. Thermal stratification and deoxygenation of the hypolimnion was found in five lakes. Details of emergent and submerged aquatic plants have been included on the contour maps. Qualitative and quantitative samples were taken of plankton and bottom fauna. The present stocks of fish were examined and waterfowl were noted. All the lakes with an outlet supported eels. The Northland series contained no stocks of game fish, but in the Wellington series limited stocks of perch and trout occurred.

I. INTRODUCTION

New Zealand has well-established freshwater fisheries consisting mainly of various exotic species of Salmonidae. There are small self-supporting stocks of other species established usually in restricted waters, of which perch (*Perca fluviatilis* L.) are widely distributed and are significant in anglers' catches in some waters. They are, however, not as often fished for by anglers as brown and rainbow trout (*Salmo trutta* L. and *S. gairdnerii* Richardson) or quinnat and atlantic salmon (*Onchorhynchus tschawytcha* (Walbaum) and *Salmo salar* L.).

In New Zealand over the past few years there has been a large increase in the number of angling licences sold. No direct index of the increase or decrease in the number of persons fishing each season was available, but an approximate measure was given by the licence revenue received.

The licence revenue for the 1936-37, 1946-47, and 1951-52 fishing seasons for New Zealand was approximately £15,600, £19,000, and £34,000. Allowance has been made for the increase in licence fees from 25/- to 30/- or 40/- a season and the revenue has been calculated on a 1936-37 value basis. Even so, there was an increase in licence revenue between 1937 and 1947 of 22 per cent. and a further increase of 79 per cent. by 1952. The map (Fig. 1) shows the licence revenue for the Auckland and Wellington Acclimatization Societies on a 1936-7 licence value basis. Figure 1

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* Fisheries Research Laboratory, Marine Department, Wellington, N.Z.

† Botany Division, Department of Scientific and Industrial Research, Wellington, N.Z.

also shows the distribution of anglers fishing in the Rotorua and Taupo Acclimatization Districts—the main tourist districts—during the 1951-1952 season. It is noticeable that at Rotorua 44 per cent. of the anglers are from the Auckland Acclimatization Society's district, whilst at Taupo 24 per cent. are from Auckland and 32 per cent. from the Wellington Acclimatization Society's district. This increase has meant much added angling pressure on the available fishing waters because little additional water has been opened to angling during this period. In New Zealand there are many waters, both lakes and rivers, which do not have self-supporting stocks of game fish. These waters are more common in the North Island.

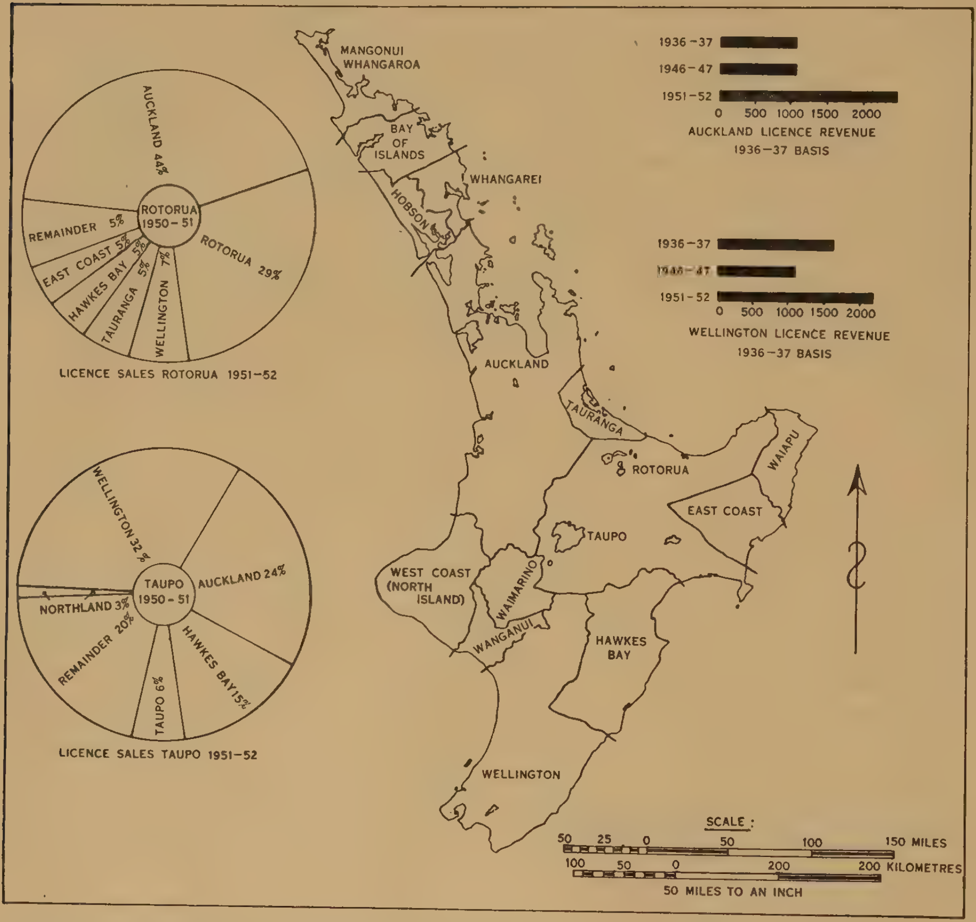

MANGONUI
WHANGAROA
BAY OF ISLANDS
WHANGAREI
HOBSON
AUCKLAND
TAURANGA
ROTORUA
WAIAPU
EAST COAST
TAUPO
WEST COAST (NORTH ISLAND)
WAIMARINO
WANGANUI
HAWKES BAY
WELLINGTON
1936–37
1946–47
1951–52
0 500 1000 1500 2000
AUCKLAND LICENCE REVENUE
1936–37 BASIS
1936–37
1946–47
1951–52
0 500 1000 1500 2000
WELLINGTON LICENCE REVENUE
1936–37 BASIS
ROTORUA 1950–51
AUCKLAND 44%
ROTORUA 29%
WELLINGTON 7%
TAURANGA 5%
HAWKES BAY 5%
EAST COAST 5%
REMAINDER 5%
LICENCE SALES ROTORUA 1951–52
TAUPO 1950–51
WELLINGTON 32%
AUCKLAND 24%
HAWKES BAY 15%
TAUPO 6%
REMAINDER 20%
NORTHLAND 3%
LICENCE SALES TAUPO 1951–52
SCALE:
50 25 0 50 100 150 MILES
100 50 0 200 200 KILOMETRES
50 MILES TO AN INCH

Fig. 1.—Distribution of anglers fishing at Rotorua and Taupo from North Island acclimatization societies' districts, and the comparative licence revenue figures for the Wellington and Auckland Acclimatization Societies.

On the West Coast of the North Island there is an extensive series of dune lakes which, in general, lack species of game fish. A few support good stocks of perch, while in some, small stocks of rainbow trout are maintained by artificial liberations.

The lakes may be conveniently grouped into two different series:

(i) A Northland series comprising about 70 lakes from Waiuku to North Cape, from 1 to 350 ac in area.

(ii) A Wellington series of about 100 lakes from 1 to 640 ac, between Otaki and Hawera.

The map (Fig. 2) shows the locality of the two series of lakes.

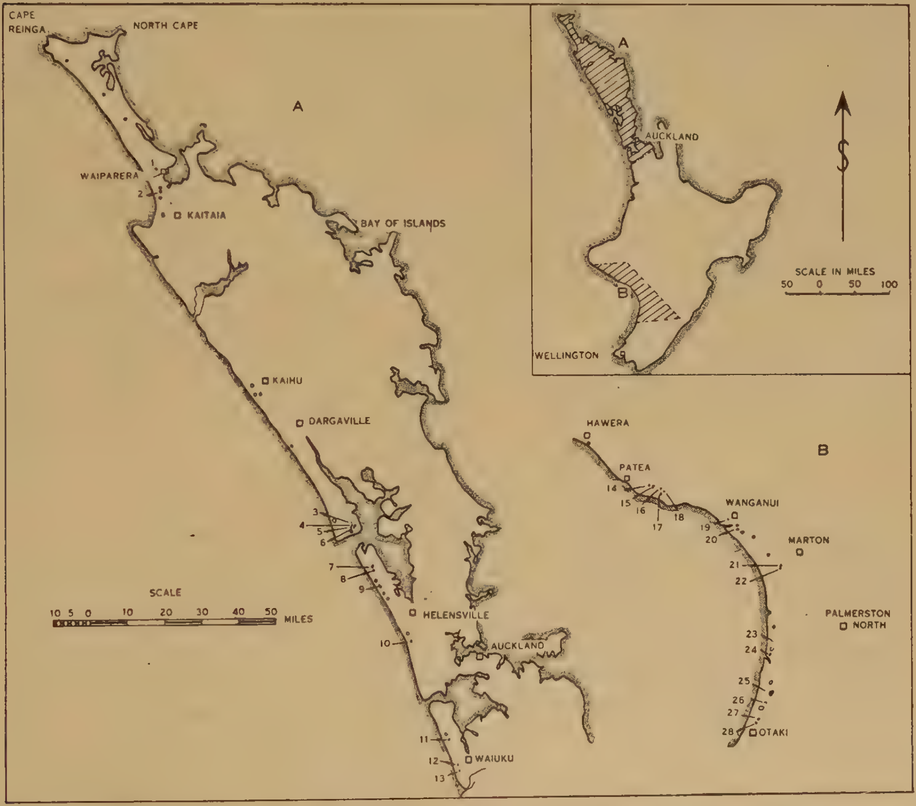

CAPE REINGA
NORTH CAPE
A
WAIPARERA
1
2
KAITAIA
BAY OF ISLANDS
KAIHU
DARGAVILLE
3
4
5
6
7
8
9
SCALE
10 5 0 10 20 30 40 50 MILES
HELENSVILLE
10
AUCKLAND
11
12
WAIUKU
13
A
AUCKLAND
B
WELLINGTON
SCALE IN MILES
50 0 50 100
HAWERA
PATEA
14
15
16
17
18
WANGANUI
19
20
MARTON
21
22
B
PALMERSTON NORTH
23
24
25
26
27
28
OTAKI

Fig. 2.—Locality map of the North Island showing the lakes surveyed in the Northland (A) and Wellington (B) series. Surveyed lakes are numbered.

This paper describes a lake surveying programme organized by the Fisheries Research Laboratory of the Marine Department to assess these series of lakes for fisheries development.

The development of the western dune lakes would help relieve the fishing pressure on the present available waters. It would also greatly increase the amount of fishing water in some acclimatization districts, particularly those in Northland, where at present little or no angling is available.

Although some of these lakes have a doubtful angling potential, they are important waters for game birds.

(*a*) *Types of Lakes*

All the lakes of both series have in common the feature of an impounding barrier of sand. The lakes of the Northland series are located amongst consolidated dunes of three distinct series of sands. Ferrar (1934) considers that the sands in the vicinity of Kaipara Harbour, as far south as Muriwai, form two distinct series. The older series (which give a yellowish brown clay on erosion) he calls the Kaihu Sands and considers to be older Pleistocene in age. The other series he considers younger Pleistocene. These sands are nearer the coast and are being covered by drifting sand. They are dark grey and less consolidated. The most recently consolidated sands near Waiuku are blackish brown in colour. The Wellington series are formed at the junction of the dune belt and older geological formations, the lakes of the Horowhenua Plain area being at the base of the Horowhenua sandstone upland. The lakes of both series may be grouped into basin and valley lakes.

(i) *Basin Lakes.*—Basin lakes are formed by the accumulation of rainwater in the dune complexes and are usually shallow, although they may be of considerable area. The surrounding country is normally of low relief and the lakes tend to be oval or elongated in shape. There are two types of basin lakes:

(1) Formed in hollows in the older consolidated dunes, e.g. Lakes Waingata, Rotokawau, and Brewer.

(2) Formed between the consolidated dunes and the moving dunes on the foreshore, e.g. Lakes Horowhenua, Kanono, and Kereta.

(ii) *Dammed Valleys.*—Many streams draining the consolidated dunes have been blocked by drifting sands. Near the junction of the sands and consolidated dunes are many such valley lakes, which are long, narrow, and usually deeper than basin lakes. The valley sides are steep and the surrounding country much higher than is normal for basin lakes. They vary considerably in size and in shape, and often consist of two or more long, narrow arms. Lakes Rototoa, Kuwakatai, Papaitonga, and Waitawa are examples.

(*b*) *Drainage of Lakes*

Few of the Northland lakes have outlet streams. The springs of the westland scarp are considered by Ferrar to be the underground drainage of some lakes. A strong spring flows into Lake Kanono from beneath recently blown sands, and this probably drains some previous swamp area, now filled with drift sand. Raupo (*Typha muelleri* Rhorb.) is still growing at the lake edge through this freshly deposited sand. The majority of the Wellington series have outlet streams although some of these are small and shallow with an intermittent flow.

(*c*) *Biological Survey*

A biological survey of sample lakes from each series was made in midsummer when the lake levels were low and adverse temperature effects and thermal stratification would be maximal.

Between January 11 and February 1, 1949, a team of five officers of the Fisheries Laboratory surveyed 13 lakes of the Wellington series, with a total area of 1,160 ac. Thirteen further lakes, totalling 1,470 ac, of the Northland series were surveyed between January 20 and February 21, 1950. In 1950, the personnel consisted of six officers of the Fisheries Laboratory, assisted by Mr. N. T. Moar of the Botany Division, Department of Scientific and Industrial Research, and Mr. R. W. Balham of the Wildlife Branch, Internal Affairs Department.

The bathymetric and general survey work was supervised by the senior author. The chemical analysis was done in 1949 by Mr. P. J. Parr and in 1950 by Mr. A. W. Torrie, and the shore-line surveys were made by Mr. P. J. Burstall. Mr. Moar accompanied the bathymetric team, identified the submerged aquatics, and mapped the emergent vegetation. Mr. Balham made observations on the density of waterfowl, their food supplies, and suitability of habitat.

A small 8-ft dinghy and, as an auxiliary, a one-man rubber boat, were used to survey the Wellington series. On the Northland series a lightweight 11-ft dinghy was also carried.

(*d*) *Selection of Lakes*

As the time available for the field survey was limited, a selection had to be made of a sample series of lakes. Good road access was necessary as each survey was planned to cover the maximum geographical area. Where convenient within each series the lakes were chosen so that the range surveyed was representative of all sizes of waters. Lakes were selected for which aerial photographs were available.

III. METHODS

At each lake surveyed, physical, chemical, botanical, and zoological surveys were made.

(*a*) *Physical Survey*

(i) *Mapping.*—A series of "markers", each consisting of a square of white cloth painted with a black cross and mounted on a frame, was set up on or near the lake shore at places convenient for the surveyors and the bathymetric teams. Bearings were taken with a theodolite on the markers and also on readily identifiable shore points from fixed base lines. Often more than one base line was required. Panoramic photographs were taken at the same time.

(ii) *Bathymetric.*—Survey lines were rowed between the markers and all soundings were taken by hand, using a heavy cord line marked in half metres. The line was weighted by a plant grab in the form of a lead sinker, which had six sharpened spikes attached, so arranged as to collect samples of any plants growing on the lake bed. Some particularly bad weather was experienced on occasions and some plant material collected may have been dislodged on the return journey of the grab. Rough water, high cross winds, and the drag of the log often made the rowing of straight survey lines difficult.

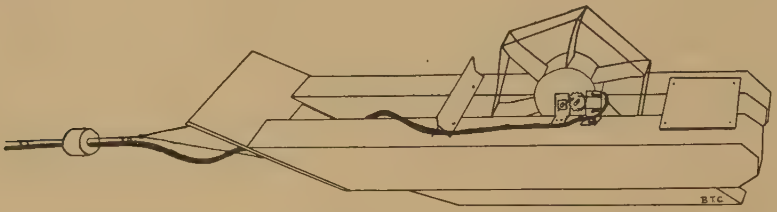


Fig. 3.—Diagram of the mechanical log. When in use, the paddle wheel and gear mechanism were covered by a light metal hood.

The even spacing of soundings in the Wellington series was achieved by trailing a pair of small boats, one ½ ch (10 m) and the other 1 ch (20 m) behind the dinghy. As the boat passed a small buoy a sounding was taken and another buoy released. The buoys consisted of sealed, waxed drinking straws, so weighted with lead shot as to float vertically, about one-third out of the water. This method was not entirely suitable and much difficulty was experienced when beginning a survey line, particularly off a weedy shore. The boats required very slow rowing speeds to float with maximum efficiency. The buoys floated well under varying conditions, but tended to drift quickly in high winds and in rough water.

On the Northland series a mechanical log was towed behind the survey dinghy. This log (Fig. 3) consisted of a six-bladed paddle wheel carried between two wooden floats with a splash deflector fitted across their forward ends. For sounding, the paddle-wheel was geared to operate a buzzer at ½- or 1-ch intervals. This spacing was controlled by a two-way switch in the dinghy. Wind effects were reduced by a light metal hood which completely covered the paddle wheel. The splash deflector tended to stop the bow dipping too deeply into the water in heavy waves.

This log was entirely satisfactory and even spacings on each run were achieved, although upwind and downwind spacings were not always the same. The electrical system sometimes gave trouble.

(iii) *Temperature.*—Temperature measurements were made in 1949 with a continuous-reading electrical thermometer, standardized by means of a mercury centigrade thermometer. Temperature changes, given by the changes of resistance in a copper coil, were read directly from a scale.

The resistance thermometer was lent by Professor Percival of Canterbury University College and is further described in a report by Parry (unpublished data 1949) to the North Canterbury Acclimatization Society. The resistance thermometer was used initially on the Northland series, but as the depths of water encountered exceeded the length of watertight cable, measurements were made with a centigrade mercury thermometer. Water samples were collected in the water sampler described later, and as soon as the sampler returned to the surface the temperature was taken. As the sampler held a considerable volume of water it was unlikely that there would have been any significant change in the temperature of the water during the short time which usually elapsed whilst the sample was being brought to the surface.

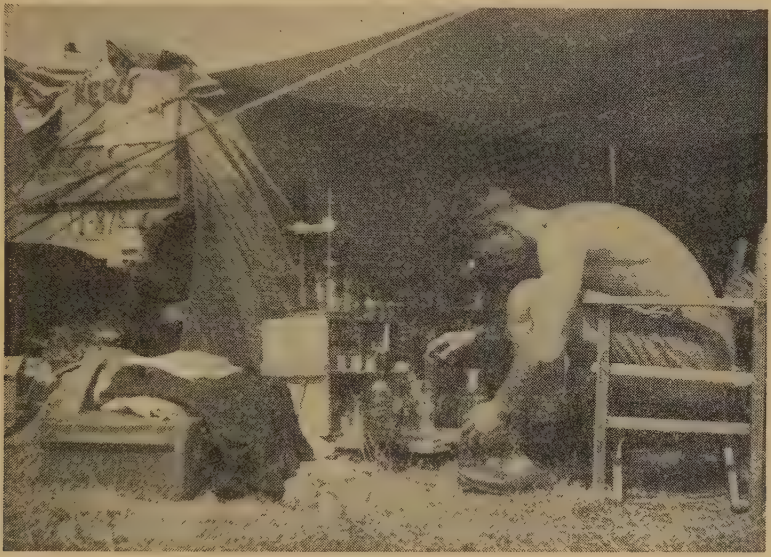


Fig. 4.—Water analysis, using the portable kit in a typical situation. (Photo: A. W. Torrie.)

(iv) *Transparency.*—A white 1-dm Secchi disc was used in both surveys.

(*b*) *Chemical Survey*

All analyses were made under field conditions on shore in the open, and Figure 4 shows a typical location. In 1949 they were restricted to pH, oxygen, silicate, and phosphate determinations. Carbon dioxide, free ammonia, nitrate, and chloride were also analysed in 1950.

On the Wellington series it was not possible to take the samples at a standard time, as they were collected and analysed when the physical survey was completed. On the Northland series an attempt to standardize the sampling time at between 1000 and 1100 hr could not be followed because of inclement weather and the varying length of time spent at each lake.

The water samples in 1949 were collected in displacement jars consisting of weighted pint milk bottles. A rubber tube which closed the widely separated inlet and outlet tubes was pulled off at the required depth by a mechanical release. The water sampler used in 1950 was cylindrical in construction with semicircular shutters at both ends. The shutters opened when the sampler was allowed to sink through the water and automatically closed when the sampler's movement was arrested, so that samples could be taken at any desired depth. It was proposed to fill reagent bottles directly from the water sampler for the oxygen analysis. The displacement bottles (used by Parry) and the water sampler were lent by Professor Percival, of Canterbury University College.

An exploratory experiment was carried out in the Laboratory to test whether any special precautions were necessary. Water from the city supply was boiled until all the air had been driven out. Two reagent bottles were filled; one carefully, with no bubbling (*A*), the other (*B*) with much bubbling. The oxygen content was measured by Winkler's method. No oxygen was detected in *A*, whilst only 0.5 ml/l was found in *B*. As this error was acceptable, 250-ml reagent bottles were filled directly from the water sampler with a minimum of bubbling.

The most commonly used standard reagents were made up in the field by diluting concentrated B.D.H. standard solutions with distilled water. This proved to be a successful way of carrying both corrosive and sensitive stock solutions.

(i) *Oxygen.*—On the Wellington series the water samples for oxygen determinations were collected under liquid paraffin to prevent any change in oxygen concentration owing to the initial high pressure within the bottle. The dissolved oxygen was fixed and then for analysis a single sample was drawn off. Oxygen concentrations were determined by the standard Winkler method. Winkler's method was again used on the Northland series, and the necessary reagents were added immediately to samples taken from the sampler. The analysis was completed as soon as the boat returned to shore. Initially samples were double-checked, but as there appeared to be no significant difference between the two results, single titrations were used.

(ii) *Silicate.*—Silicate was estimated as silicon dioxide by the Atkins (1923) modification of Dienert and Wandenbulck's colorimetric method. This type of estimation was again modified in the Northland series as the picric acid standard was found unsatisfactory under field conditions. Consequently a set of permanent potassium chromate standards, as described by the American Public Health Association (1946), was used. These standards had a range of from 2 to 20 p.p.m., advancing by units of two, and were found to be most satisfactory.

(iii) *Phosphate.*—Phosphate was estimated as phosphorus pentoxide by the Atkins (1925) modification of Denige's method.

(iv) *Hydrogen Ion Concentration.*—pH was measured on a Galileo-Hellige comparator, using glass standards. The indicator solutions used were bromo-cresol purple for the 5.2-6.8 range, and phenol red for the 6.8-8.4 range. Readings were taken as soon after sampling as possible, some being taken in the boat.

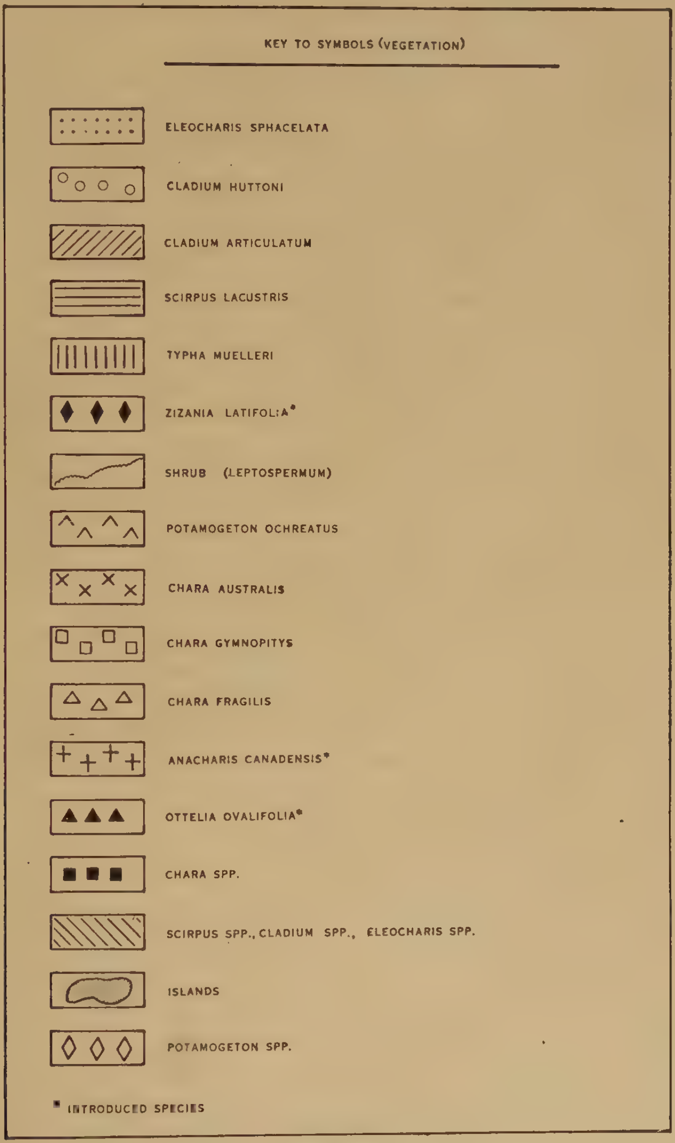

KEY TO SYMBOLS (VEGETATION)
ELEOCHARIS SPHACELATA
CLADIUM HUTTONI
CLADIUM ARTICULATUM
SCIRPUS LACUSTRIS
TYPHA MUELLERI
ZIZANIA LATIFOLIA*
SHRUB (LEPTOSPERMUM)
POTAMOGETON OCHREATUS
CHARA AUSTRALIS
CHARA GYMNOPITYS
CHARA FRAGILIS
ANACHARIS CANADENSIS*
OTTELIA OVALIFOLIA*
CHARA SPP.
SCIRPUS SPP., CLADIUM SPP., ELEOCHARIS SPP.
ISLANDS
POTAMOGETON SPP.
* INTRODUCED SPECIES

Fig. 5.

(v) *Carbon Dioxide.*—The method followed was that outlined by Welch (1948). This method was slightly modified in view of some comparative work carried out by Peters, Williams, and Mitchell (1940), as a considerable error arises if the normal end-point reading is used in this type of titration. Accordingly, their method of using the lingering pink colour, which persists for some 2-3 sec before the permanent change in colour occurs, was adopted.

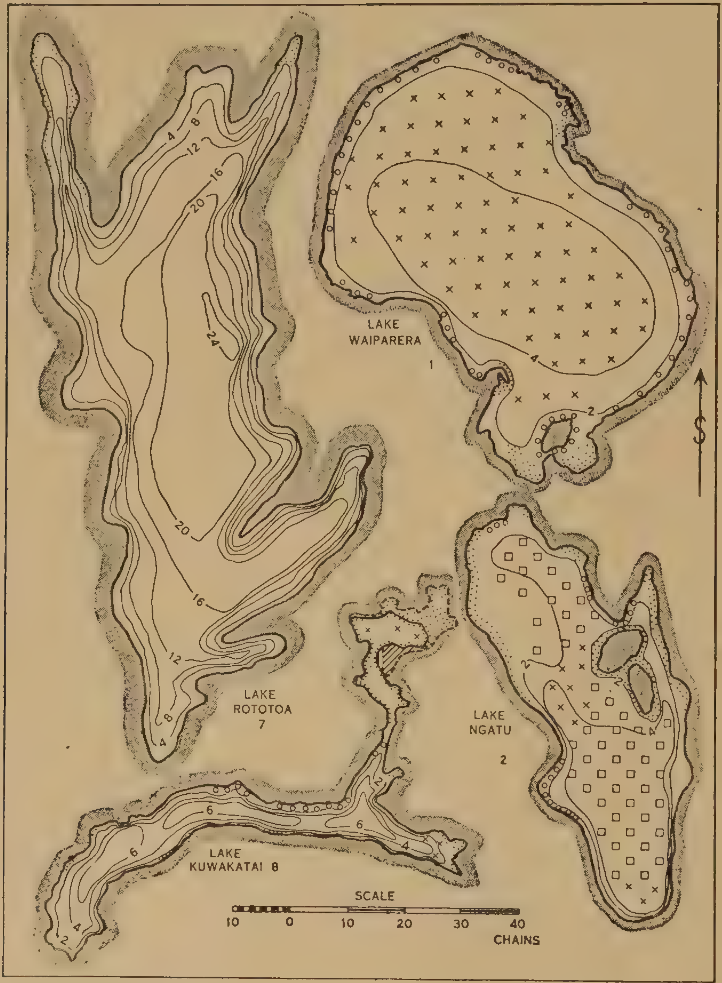

LAKE WAIPARERA
1
LAKE ROTOTOA
7
LAKE NGATU
2
LAKE KUWAKATAI 8
4
8
12
16
20
24
20
16
12
8
4
2
6
6
6
4
4
2
2
SCALE
10
0
10
20
30
40
CHAINS

Fig. 6.—Vegetation and contoured maps of lakes of the Northland series. Contour interval 2 m, except Lake Rototoa (4 m).

(vi) *Chloride.*—The Mohr method as described by the American Public Health Association (1946), was used and found to be satisfactory under field conditions.

(vii) *Nitrates.*—Nitrates were estimated as nitrate by the phenoldisulphonic acid method, although it proved to be cumbersome for field analyses. The time required for evaporations made it necessary to hold samples over and analyse them in batches of four. The activity of oxidizing microorganisms during the 2-4 days the samples were held was reduced by adding 5 ml of conc. sulphuric acid to each 100-ml sample.

(viii) *Free Ammonia.*—The direct Nesslerization of samples was employed and it appeared to give satisfactory results.

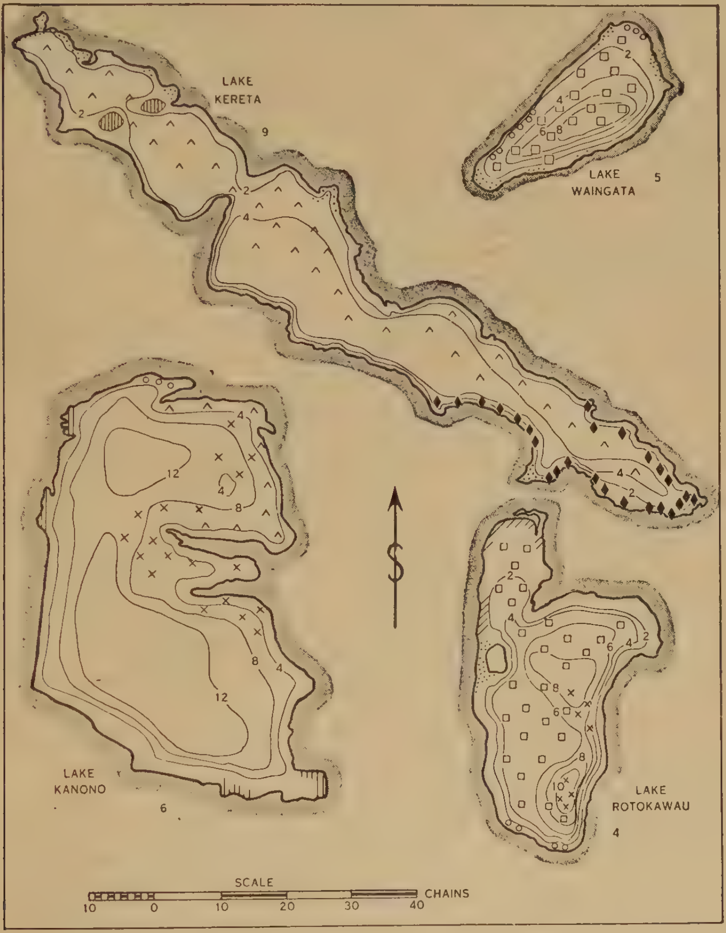


Fig. 7.—Vegetation and contoured maps of lakes of the Northland series. Contour interval 2 m, except Lake Kanono (4 m).

(ix) *Inorganic Residues.*—A water sample from Lakes Okaihau, Swan, Kuwakatai, and Ngatu of the Northland series was analysed at the Dominion Laboratory, Wellington, for the nature of inorganic residues.

(*c*) *Botanical Survey*

Limited botanical observations were made on the Wellington series. In the field, outline maps were used to mark the distribution of the emergent vegetation on the Northland series. Submerged vegetation was collected by the plant grab, the samples being taken when the soundings were made. These data have been included on the contour maps on Figures 5-10.

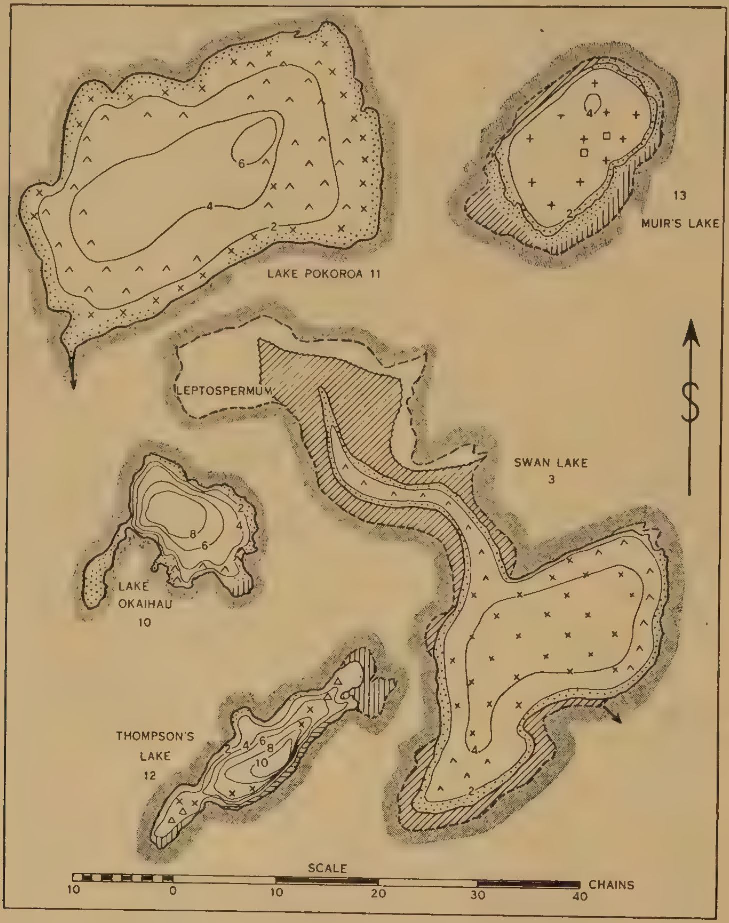

LAKE POKOROA 11
2
4
6
13
MUIR'S LAKE
2
4
LEPTOSPERMUM
SWAN LAKE
3
2
4
LAKE
OKAIHAU
10
2
4
6
8
THOMPSON'S
LAKE
12
4
6
8
10
SCALE
10
0
10
20
30
40
CHAINS

Fig. 8.—Vegetation and contoured maps of lakes of the Northland series. Contour interval 2 m.

(*d*) *Zoological Survey*

Plankton, invertebrate, and fish collections were made.

(i) *Plankton.*—The plankton was sampled in 1949 by means of small nets. The two nets used had a diameter of 10 in. and were of 60 and 150 meshes/in. respectively. A single surface tow of 5 min duration was made with each net at each lake. In 1950 a semirotary pump was used and the plankton was sieved by a gravity feed system. A standard volume of 9 l. was sieved.

(ii) *Invertebrates.*—Invertebrates were sampled by dredging, hand-netting, and by Petersen grab samples. Visual observations were also made.

(iii) *Vertebrates.*—Two standard eel traps (Burnet 1952), two fyke nets, and two 3-in. mesh gill nets, 66 yd by 8 ft 6 in. deep, were used. Where shore conditions and weed beds permitted, seine nets were operated, their dimensions being 60 yd by 8 ft 6 in. deep, with 2-in. mesh, or 30 yd by 8 ft 6 in. deep, with 1⅛-in. mesh. Eels were also gaffed and hand-net collections made.

(iv) *Waterfowl.*—Waterfowl and game birds were recorded.

IV. Physical Features

(*a*) *Morphometry*

The contour maps (Figs. 6-10) have been drawn from the bathymetric and mapping data. To aid in the shore-line demarcation, enlargements from aerial photographs have been used in conjunction with the photographic panoramas. The number of soundings taken was limited, but they were considered sufficient to give a general picture of the lake bottom.

The morphometric detail is given in Table 1. The lake area has been calculated from planimeter measurements on the outline maps, and the volume by the formula given in Welch (1948). The maximum depth recorded by the team may not be the absolute maximum depth of each lake. The mean depth is the lake volume divided by the area.

Lake Horowhenua, the largest lake surveyed, was about 640 ac, and only seven of the lakes exceeded 100 ac in area. Lake Rototoa, the deepest lake, had a maximum depth of 29 m, but only six others exceeded 10 m. The Northland series were larger and deeper than the Wellington series. All the lakes are, however, comparatively small and shallow.

(*b*) *Temperature*

Figure 11 shows the variation of temperature and oxygen content of the different lakes plotted against depth, for both surveys. Air temperatures are included where these were taken. Surface temperatures varied between 18° and 24°C. As Lake Pukepuke was less than 1 m deep, only the surface temperature (18.5°C) was taken. The lakes of the Wellington series are all shallow and little change of temperature with depth was noted. In three lakes only—Lakes Waitawa, Kopureherehe, and Westmere—were conditions suggestive of the presence of a thermocline noted. In Lake Westmere there was a drop of 8°C in 4 m. This lake is very sheltered from wind, being completely surrounded by trees. Lakes Waitawa and Kopureherehe had a thermocline between 3 and 4 m and 4 and 5 m respectively. These lakes were the least exposed of the series. Complete turnover by wind occurred in all the remaining lakes.

In the Northland series it will be noticed that oxygen content follows the temperature readings fairly consistently. Only in Lake Okaihau was

TABLE 1

MORPHOMETRY OF LAKES

Type of lake: BC = basin lake in consolidated sands; B = basin lake between unconsolidated and consolidated dunes; D = dammed valley. Inlet or outlets: N = nil; T = temporary; P = permanent. Thermocline: A = absent; P = present. Designation of lakes as in Figure 2

Lake	Date	Designation	Type of Lake	Area		Volume		Max. Depth		Mean Depth		Thermocline	Inlet	Outlet
				100 Sq. m.	Ac	100 Cu. m.	1000 Cu. Ft.	m	Ft	m	Ft			
Northland series														
Waiparera	18-21.ii.50	1	B	11,740	290.0	37,536	13,250	5.8	17.5	3.2	10.6	A	P	P
Ngatu	15-17.ii.50	2	BC	6,219	154.0	10,429	3,690	6.0	19.8	3.0	9.9	A	N	N
Swan	7-8.ii.50	3	D	1,720	42.5	5,517	1,950	5.5	18.3	3.2	10.6	A	N	T
Rotokawau	8-9.ii.50	4	BC	3,428	84.7	14,826	5,240	12.0	39.6	4.3	14.3	A	N	N
Waingata	8-9.ii.50	5	BC	1,431	35.6	5,816	2,060	9.5	31.4	4.0	13.3	—	N	N
Kanono	9-10.ii.50	6	B	7,774	192.0	61,481	21,700	15.5	51.0	7.9	26.0	A	N	N
Rototoa	3-5.ii.50	7	D	13,812	341.0	168,660	59,500	29.0	95.6	12.2	40.3	A	N	N
Kuwakatai	1-3.ii.50	8	D	2,890	71.4	17,898	6,320	15.0	49.5	6.2	20.4	A	N	N
Kereta	31-1.ii.50	9	B	5,999	148.2	19,816	7,000	5.0	16.5	3.3	11.0	A	N	N
Okaihau	28-29.i.50	10	B	472	11.7	1,859	656	9.5	31.4	4.8	15.7	A	P	P
Pokoroa	25-27.i.50	11	B	2,809	69.4	7,191	2,540	4.5	14.8	2.6	8.6	P	N	N
Thompson's	24-25.i.50	12	D	449	11.2	1,908	675	11.0	36.3	4.2	13.9	A	N	P
Muir's	23-24.i.50	13	BC	634	15.6	1,362	480	4.0	13.4	2.2	7.3	P	P	P
Wellington series														
Oturi	29-30.i.49	14	BC	1,162	28.7	3,919	1,390	6.5	21.4	3.4	11.2	A	N	P
Herengawe	27-28.i.49	15	D	1,297	32.7	6,209	2,200	6.5	21.4	4.8	15.8	A	N	N
Waiau	24-26.i.49	16	D	2,743	67.8	3,990	1,340	3.3	10.4	1.4	4.6	A	P	P
Okoia	27.i.49	17	D	—	—	—	—	5.0	16.5	—	—	—	P	P
Brewer's	26.i.49	18	BC	215	5.3	885	311	6.9	22.7	4.1	13.5	A	N	N
Westmere	23-24.i.49	19	D	757	18.7	1,972	695	6.0	19.6	2.6	8.6	P	P	P
Pauri	22.i.49	20	D	—	—	—	—	12.5	41.3	—	—	—	N	P
Heaton	21.i.49	21	D	1,198	29.6	2,005	705	4.3	14.0	1.7	5.6	A	N	P
Bernard	20-21.i.49	22	D	822	20.3	—	—	7.3	24.0	—	—	A	N	N
Pukepuke	19-20.i.49	23	B	1,631	40.3	340	120	0.6	2.1	0.2	0.7	A	N	T
Foxton No. 1	17-18.i.49	24	B	1,858	45.9	1,430	505	3.2	11.5	1.0	3.3	A	P	P
Horowhenua	15-16.i.49	25	B	—	640.0	—	—	2.0	6.6	—	—	A	P	P
Papaitonga	13-14.i.49	26	D	6,560	161.2	7,627	2,700	2.8	9.1	1.2	4.0	A	P	P
Kopureherehe	16-17.i.50	27	D	785	19.4	5,073	1,790	12.0	39.8	6.6	21.8	P	N	T
Waitawa	11-13.i.49	28	D	1,781	44.0	6,893	2,450	7.8	25.6	3.9	12.9	P	P	P

stratification present at the time of the survey, the thermocline being between 2 and 6 m. This lake was well sheltered from all winds in a protected hollow in old stable sand dune country. The deeper lakes, Rototoa, Kuwakatai, Kanono, and Rotokawau, showed very little range in temperature throughout their depths. All these lakes have very much the same physical configuration, the longitudinal axis of each lake being exposed to the prevailing north-west wind. The unusually high temperature recorded at 25 m in Lake Rototoa suggests that recent high winds must have caused almost complete mixing. The overturn of water at Lake Rotokawau was even more obvious as the temperature difference between the surface and the bottom at 10 m was only 0.6°C. When samples were taken in this lake the waves were running to an estimated 78 cm in height, and were breaking.

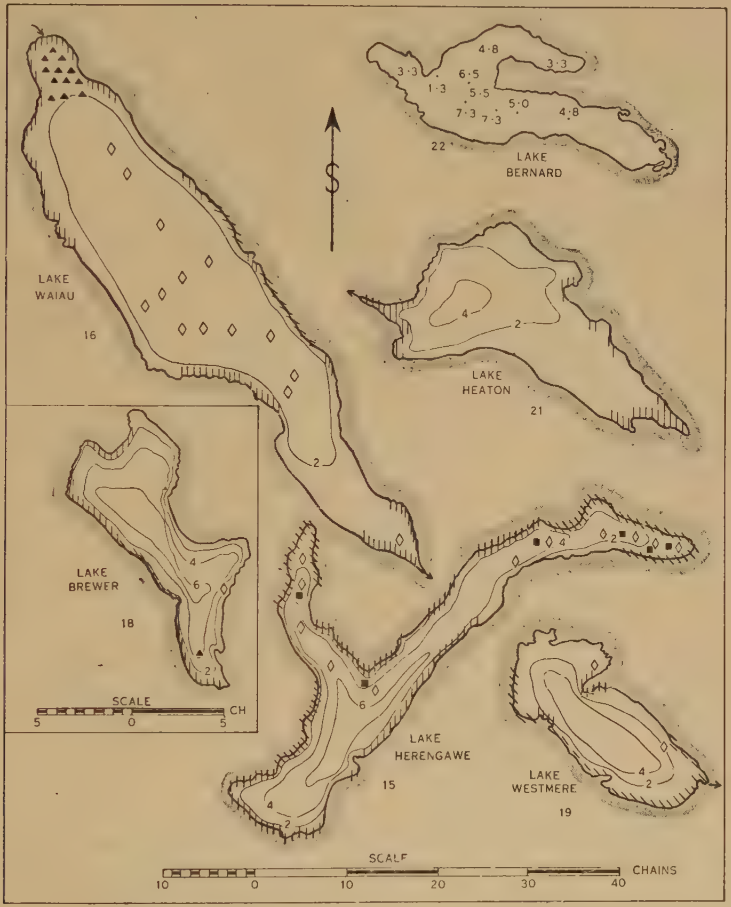

LAKE WAIAU
16
2
4·8
3·3
3·3
6·5
1·3
5·5
5·0
7·3
7·3
4·8
22
LAKE BERNARD
4
2
LAKE HEATON
21
LAKE BREWER
18
4
6
2
SCALE
5
0
5
CH
2
4
6
LAKE HERENGAWE
15
4
2
4
2
LAKE WESTMERE
19
SCALE
10
0
10
20
30
40
CHAINS

Fig. 9.—Vegetation and contoured maps of lakes of the Wellington series. Contour interval 2 m.

(*c*) *Transparency*

Secchi disc readings given in Tables 3 and 4 were low in all lakes, except Lakes Rototoa and Kuwakatai of the Northland series. In the shallower lakes the silt and bottom sediments were disturbed by the wind.

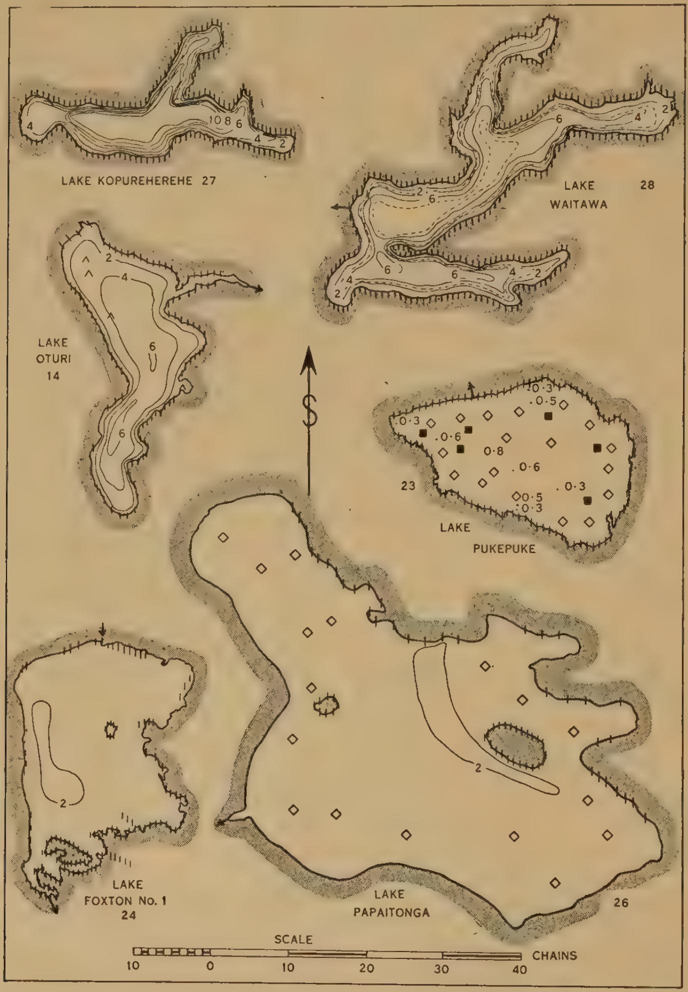

10 8 6
4
2
4
LAKE KOPUREHEREHE 27
6
4
2
2
6
6
6
4
2
2
4
LAKE WAITAWA
28
2
4
6
6
LAKE OTURI
14
0·3
0·5
0·3
0·6
0·8
0·6
0·3
0·5
0·3
23
LAKE PUKEPUKE
2
LAKE FOXTON No. 1
24
2
LAKE PAPAITONGA
26
SCALE
10
0
10
20
30
40
CHAINS

Fig. 10.—Vegetation and contoured maps of lakes of the Wellington series. Contour interval 2 m.

V. Chemical Features

(*a*) *Oxygen*

Figure 11 shows the distribution of oxygen concentration and of temperature with depth. Table 2 gives the percentage oxygen saturation against depth.

Surface oxygen concentrations varied between 5.8 and 9.0 ml/l. At Lake Pukepuke only the surface concentration of 7.2 ml/l was measured. Oxygen concentration was fairly evenly distributed throughout the lake depth in the Northland series whereas in the Wellington series the surface concentrations tended to be the highest. Deoxygenation of the deeper waters occurred in five lakes. Lakes Waitawa, Kopureherehe, Westmere, and Okaihau were stratified and had an oxygen-deficient hypolimnion.

TABLE 2

PERCENTAGE OXYGEN SATURATION

Lake	Depth (m)							
	0	2	4	6	8	10	15	25
Northland series								
Waiparera	107	107						
Ngatu	108	108	108					
Swan	103	103	102					
Rotokawau	100		99			80		
Kanono	120	120	120	117	117	100		
Rototoa	110	110	110	109	109	105	93	55
Kuwakatai	103	102	100	100	100	97		
Kereta	110	110	109					
Okaihau	95	87	30	10	0	0		
Pokoroa	100	96	95					
Thompson's	100	100	98	86	20	15		
Muir's	102	102	100					
Wellington series								
Oturi	96	97						
Herengawe	98	95		95				
Waiau	98	103						
Brewer's	125	108						
Westmere	152		15					
Heaton	105	104	75					
Pukepuke	108							
Foxton No. 1	87	65						
Horowhenua	118	65						
Papaitonga	93	63						
Kopureherehe	110	102	100	29	25	13		
Waitawa	150	10			0			

In Lake Thompson the stratification may have been partially destroyed by wind, as from the surface to 6.0 m the oxygen concentration was about 4.0 ml/l, but fell to 1.0 ml/l at 10 m. In the shallow exposed lakes, and also in the deeper Lakes Kanono and Kuwakatai, water turnover was complete. At Lake Rototoa it occurred to a depth of 12 m.

Oxygen saturation values are of major concern during stagnation periods. The percentage saturation values were small in the hypolimnion of stratified lakes and in the deeper waters of Lake Thompson. Surface saturations were high, particularly so in Lakes Brewer, Westmere, and Waitawa, where they ranged from 125 to 152 per cent. and suggested the

TABLE 3

PHYSICAL AND CHEMICAL RESULTS

Lake	Date	Time	Prevailing Weather			Secchi Disc (m)	Silica (p.p.m.)	Phos-phate (p.p.m.	pH	Carbon Dioxide (p.p.m.)	Chloride (p.p.m.)	Nitrate (p.p.m.)	Free Ammonia (p.p.m.)
			Cloud	Wind	Water								
Northland series													
Waiparera	18.ii.50	1000	1	Strong	Light waves	2.5	2	0.012	6.6 SC	5.3	126.4	—	0.016
Ngatu	16.ii.50	1030	10	Light wind	Slight ripple	4.0	T	T	6.2 SC	7.0	49.3	—	0.006
Swan	8.ii.50	1000	1	Nil	Calm	2.0	2	0.016	6.2	10.5	53.4	0.05	0.006
Rotokawau	8.ii.50	1245	4	Light breeze	Slight ripple	—	T	0.010	6.4	8.2	55.8	0.08	0.010
Kanono	9.ii.50	1100	4	High wind	Heavy waves	4.6	2	0.020	6.6	5.3	29.0	0.10	T
Rototoa	4.ii.50	1100	3	Nil	Calm	9.0	4	0.016	6.6 SC 6.4 SB	6.3 SC 6.0 CB	58.2	0.20	0.060
Kuwakatai	2.ii.50	1130	1	Nil	Calm	7.0	2	0.010	6.6 SC	8.8	72.8	0.10	0.001
Kereta	31.i.50	1430	2	Light breeze	Slight ripple	3.0	2	T	6.4 SC	1.8	94.6	0.14	T
Okaihau	28.i.50	1100	1	Light breeze	Calm	2.0	20	0.030	6.5 SC 6.3 CB	3.5 SC 14.2 CB	84.9	0.24	T
Pokoroa	25.i.50	1600	10	Strong	Very rough	1.0	15	0.010	6.6 SC 6.4 SM	5.0	—	0.05	0.004
Thompson's	25.i.50	0800	3	Nil	Ripple	2.5	2	0.010	6.3 SC	1.8	—	—	T
Muir's	23.i.50	1145	5	Nil	Calm	2.0	6	0.020	6.6 SC 6.4 SM	4.4	—	T	0.005
Wellington series													
Kopureherehe	17.i.50	0745	1	Nil	Calm	1.5	2	T	6.5 SC 5.9 CB	12.0	—	0.10	0.014

SC = surface centre; SM = surface margin; CB = centre bottom; T = trace.

need for further examination. A phytoplankton bloom (Moore 1950), green plants (Phelps 1947), or a sudden increase of surface temperature (Brett 1950) may cause high supersaturation.

From Appendix I it can be seen that the presence of large quantities of organic matter or of certain inorganic radicals can give a false value for oxygen concentration when the unmodified Winkler method is used. At Lakes Brewer, Waitawa, and Westmere the use of the normal Winkler method probably gave the very high percentage saturation value.

TABLE 4

PHYSICAL AND CHEMICAL RESULTS — WELLINGTON SERIES

Lake	Date	Secchi Disc (m)	Silica (p.p.m.)	Phosphate (p.p.m.)	pH
Oturi	29.i.49	1.75	3.0	0.010	8.0
Herengawe	28.i.49	2.00	8.0	T	8.0
Waiau	24.i.49	2.5+ (bottom)	15.0	0.025	8.4+
Okoia	27.i.49	2.00	14.0	0.020	8.0
Brewer's	25.i.49	1.25	2.0	T	8.4+
Westmere	23.i.49	0.66	5.0	0.030	8.4+
Pauri	22.i.49	—	0.2	0.010	—
Heaton	21.i.49	1.25	1.4	0.050	8.4+
Bernard	21.i.49	—	0.6	0.010	—
Pukepuke	19.i.49	0.50	8.0	0.013	8.4+
Foxton No. 1	17.i.49	0.50	8.0	0.010	8.4
Horowhenua	15.i.49	0.75	10.0	0.015	8.4+
Papaitonga	13-14.i.49	0.75	5.0	0.030	8.4+
Kopureherehe	13.i.49	0.75	—	—	—
Waitawa	12.i.49	0.80	4.0	0.025	7.9

(b) *Silicate*

Silicate concentrations varied between 0.2 and 20.0 p.p.m. The results vary widely, even for lakes of approximately similar character close together. The dune lakes have a much higher silicate concentration than the thermal lakes of New Zealand. Phillipps and Grigg (1922) found that the concentration of sodium silicate varied between 0.07 and 2.33 p.p.m. The values for silicate determined in the field and in the laboratory agreed quite favourably.

(c) *Phosphate*

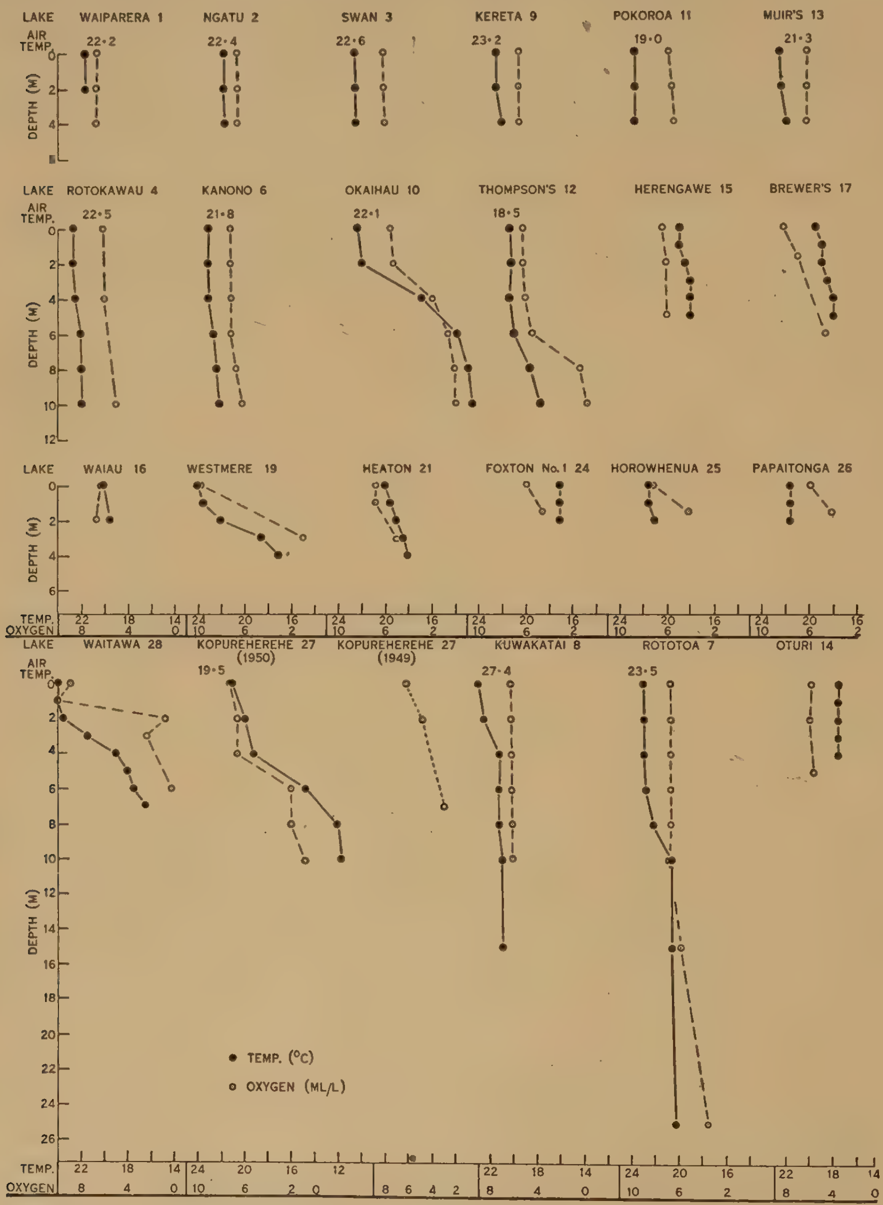
Phosphate concentrations were all low and varied between a trace and 0.030 p.p.m.

(d) *Hydrogen Ion Concentration*

The pH measurements of the Wellington series show a high alkalinity for lakes and the pH ranged from 7.9 to more than 8.4.

On August 26, 1952 the pH of Lakes Waitawa and Kopureherehe was again measured. The pH of Lake Waitawa was 7.5 and of Lake

Kopureherehe 7.0, using phenol red indicator. The results disagree markedly with the values obtained in 1949 and suggest that the high alkalinities then measured may not be the true values.



Temperature (°C) and oxygen concentration measurements from surface to near bottom, for lakes of the Northland and Wellington series.

The range in pH at the surface of the Northland lakes was between 6.2 and 6.6. Normally only the surface layers were tested and only a few bottom samples were analysed. The relatively low figures recorded were not unexpected as the marginal areas of most of these lakes were covered with decaying aquatic vegetation and, for the most part, were very peaty. The lake beds were also covered with plant remains and a considerable amount of general detritus. The area of peat was small in the larger lakes Waiparera and Kereta.

(*e*) *Carbon Dioxide*

In all these lakes carbon dioxide was determined in the surface layers of the lakes, the range extending from 1.8 p.p.m. at Lake Thompson to 10.5 p.p.m. at Lake Swan. Only one bottom sample was analysed, that being at Lake Okaihau, where the concentration was found to be 14.2 p.p.m., and this high concentration in the hypolimnion may have been caused by the lake stratification. The relative shallowness and exposure of most of the other lakes, with a resultant high degree of mixing, should tend to keep the carbon dioxide content at the bottom to a low value.

TABLE 5

INORGANIC RESIDUES (P.P.M.) — NORTHLAND LAKES

		Ngatu	Swan	Kuwakatai	Okaihau
Silica	(SiO_2)	Nil	1.8	3.4	26.4
Calcium	(Ca^{++})	4.6	6.7	6.6	8.4
Magnesium	(Mg^{++})	6.6	5.8	7.4	8.2
Sodium	(Na^{+})	34.0	31.0	28.0	52.0
Potassium	(K^{+})	3.0	3.0	3.0	3.0
Residue on evaporation (Dried at 105°C)		153	142	137	230

(*f*) *Chloride*

The concentration of chlorides ranged from 29.0 p.p.m. at Lake Kanono to 126.4 p.p.m. at Lake Waiparera. A great number of these lakes were bounded by running sand on the western, seaward margins, but there appeared to be no relationship between this factor and chloride concentration as Lake Okaihau, which was located in old stable sand dune country, had a chloride concentration of 84.9 p.p.m. Lake Wilson had running sand extending along the entire western margin and here the concentration was slightly higher at 94.6 p.p.m. The chloride content of these lakes was much higher than in the thermal lakes, for 13 of which Phillipps and Grigg (1922) found that the concentration of chlorides was less than 1.0 p.p.m., and for three others 1.7, 2.0, and 10.4 p.p.m. respectively.

(*g*) *Nitrate*

Concentrations ranged from 0.24 p.p.m. at Lake Okaihau to a trace at Lake Ngatu.

(*h*) *Free Ammonia*

Most results showed a low concentration of free ammonia. The highest figure recorded was 0.01 p.p.m. at Lake Waiparera. However, at Lake Waiparera there was contamination caused by refuse from an abattoir being emptied into the southern waters of the lake.

(*i*) *Inorganic Residues*

The analysis of samples by the Dominion Laboratory are given in Table 5.

VI. BOTANICAL FEATURES

A more extensive survey was made of the Northland series.

(*a*) *Classification of Plant Groups*

The vegetation of the Northland lakes includes several groups of plants, and a brief description of the groups may be useful.

(i) Tall flowering plants with only the lower parts submerged. Included in this group are the well-known raupo (*Typha muelleri* Rhorb.) and the round-stemmed sedges such as *Eleocharis sphacelata* R.Br., and species of *Cladium*.

(ii) Flowering plants with submerged and floating leaves, e.g. *Potamogeton cheesemanii* A. Benn.

(iii) Flowering plants with only submerged leaves, including *Potamogeton ochreatus* Raoul and *Anacharis canadensis* (Michx.) Planch.*

(iv) Algae. For the present purpose *Chara* is the only alga discussed.

(*b*) *Littoral Region*

The emergent vegetation was dominated by tall sedges. In some lakes a mosaic of dense vegetation and scattered colonies occurred, and in others a few scattered plants relieved an otherwise barren shore. These differences are related to shelter from wind and wave erosion, to the proximity of drifting sand, and to the depth of water. In sheltered situations material from marginal vegetation accumulates to form a peaty layer on which dense communities develop. In exposed positions, turbulence of the water prevents accumulation of debris and the establishment of vegetation. The dominant species of the vegetation have the common feature of being propagated by rhizomes. These underground shoots enable the plants to colonize the lakes to a limiting depth of 2 m, which prevents further growth into the water.

(i) *Exposed Shore-lines.*—Along the western shores of Lakes Rototoa, Waingata, Rotokawau, Kereta, and Kanono, and parts of other lakes, e.g. Lake Waiparera, vegetation was absent in the more exposed situations. Scattered stands of *Cladium huttoni* R.Br. occurred on exposed clay and where some sediment was able to accumulate, *Scirpus lacustris* R.Br. and *Cladium articulatum* R.Br. were sometimes found. *Typha muelleri* formed isolated colonies along some exposed shores.

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* Introduced species.

TABLE 6

PRINCIPAL SPECIES OF THE NORTHLAND LAKES

Lake	*Eleocharis sphacelata*	*Cladium articulatum*	*Cladium huttoni*	*Typha muelleri*	*Scirpus ucustris*	*Chara australis*	*Chara gymnopitys*	*Anacharis candensis**	*Potamogeton ochreatus*
Waiparera	XX	X	X	X	X	XX	X		
Ngatu	XX		X	X		XX	XX		
Swan	XX	X	X	X		XX	X		XX
Rotokawau	X	X	XX			X	XX		
Waingata	X		XX				XX		
Kanono	X		X	X	X	X			X
Rototoa	X	X		X					
(sheltered bay)	XX	X		X		XX			
Kuwakatai	X		XX		X	X	X		
(sheltered bay)	XX					XX			
Kereta	X				X	X	X		
Okaihau	X			X	X	X			XX
Pokoroa	XX			X		X			XX
Thompson's	X		X	X	XX	X	XX		
Muir's	XX	X	X	X		X	X	XX	X

XX = Dominant along some part of the shore.
X = Presence.

(ii) *Sheltered Shores.*—Lakes Muir, Pokoroa, and Swan were sheltered, and the bays in Lakes Kereta and Kuwakatai and parts of Lakes Ngatu and Waiparera were also sheltered. *Eleocharis sphacelata*, a tall sedge with red-green septate stems, which gives a characteristic appearance to the vegetation, extended to a limiting depth of 2 m. In shallower marginal waters *Cladium articulatum, C. huttoni, Typha muelleri*, and *Eleocharis acuta* R.Br. were associated with *E. sphacelata*, but with the exception of *T. muelleri* were never common under such conditions. *Cladium articulatum* was frequent on peaty areas surrounding some of the lakes.

Typha muelleri was found in a variety of environments, but was more typical of the swampy valleys leading into some of the lakes. A dense stand of *Zizania latifolia* Turcz.* was found around the southern shore of Lake Kereta, and dead bases of *Typha* found in it were evidence that this introduced species had replaced an original vegetation of *T. muelleri.*

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* Introduced species.

In a shallow, sheltered bay at Lake Kereta a dense stand of *E. sphacelata* was growing in stagnant water. In this bay the following additional species were rooted in the soft peaty substratum: *E. acuta, Polygonum* sp., *Myriophyllum propinquum* A. Cunn., and *Potamogeton cheesemanii. E. sphacelata* formed extensive open colonies in some lakes on a layer of mud several inches deep, e.g. Lake Ngatu.

Small floating mats of vegetation were found close to the margin of Lakes Muir and Pokoroa. The mats were formed from a tangle of roots and rhizomes and they supported *Eleocharis sphacelata, Typha muelleri, E. acuta, Isachne australis* R.Br., and *Juncus lampocarpus* Ehr.

The submerged vegetation was most frequently *Chara australis* and *Potamogeton ochreatus.* At Lake Muir *Anacharis canadensis** replaced these indigenous species.

(iii) *Effect of Slope.*—In the valley lakes, e.g. Kuwakatai, Okaihau, and Thompson's, the lake bottom sloped so steeply from the shore-line that water deeper than 2 m occurred close inshore. As a consequence, the emergent vegetation was restricted to a narrow marginal band or to scattered clumps of plants close to shore. *Cladium huttoni* and *Scirpus lacustris* occurred in scattered bands at Lakes Kuwakatai and Thompson, and *Eleocharis sphacelata* formed a narrow but continuous band of vegetation at Lake Okaihau.

(iv) *Drifting Sand.*—Drifting sand had destroyed the vegetation on the western shores of Lakes Kanono and Kereta. Isolated stands of *Eleocharis acuta* were growing in the firmer sand at the northern end of Lake Kereta.

(*c*) *Sublittoral Region*

The submerged vegetation in shallow water was influenced by shelter from wave action and in deeper waters by the nature of the sediments. Dense mats of vegetation were found in all except in Lakes Rototoa, Kuwakatai, and most of Lake Okaihau, three lakes with steeply sloping sides. At Lake Kuwakatai *Chara fragilis* Desv. was present in isolated clumps, but in the smaller Lake Okaihau *Potamogeton ochreatus* was growing on a shallow peat deposit. At Lake Thompson there was a scattered vegetation of *Chara australis, C. gymnopitys* A. Braun, and *C. fragilis* occurring in dense clumps where there were organic deposits. *Potamogeton ochreatus* was confined to areas with organic sediments well mixed with sand, and *Chara australis* R.Br. was restricted to areas with predominantly organic sediments. *Chara gymnopitys* was common on sand. Of these three species, *P. ochreatus* was never common in water more than 5 m deep, nor was *C. gymnopitys* in a depth greater than 8 m. *C. australis* was generally never common in water deeper than 7 m, but at Lake Rotokawau patches occurred at 12 m. Submerged vegetation tended to occur in well-defined colonies of a single species and, at the

* Introduced species.

margins of the lakes, could occur with or without accompanying emergent vegetation. Lake Pokoroa and parts of Lake Kereta, which had an organic deposit mixed with sand, were dominated by *Potamogeton ochreatus*. The plant cover appeared to be continuous, but not so dense as to exclude *Chara australis* and *C. gymnopitys*, which were sometimes dredged up with the *Potamogeton*. At Lake Muir *Anacharis canadensis** had replaced indigenous species and formed tangled mats of closely growing vegetation with occasional plants of *Chara australis* and *C. gymnopitys* growing in it. *C. australis* formed dense matted beds in Lakes Waiparera and Swan and in such small areas of Lake Kereta as were underlain by deep organic layers. *C. gymnopitys* was dominant over large areas in lakes with little or no organic deposit. At Lake Waingata this was the only species recorded, but at Lakes Ngatu and Rotokawau *Potamogeton ochreatus* and *C. australis* were occasionally present as well.

(*d*) *Vegetation and Lake Type*

The dense marginal vegetation of the basin lakes and the scattered, narrow marginal bands of vegetation of the valley lakes were characteristic of the lakes investigated.

The sheltered situations of many of the basin lakes has led to rapid growth of marginal vegetation which was able to extend into the lakes because of the shallow water. Continuous deposition of debris was important for depositing material built up the lake bed so that plants were able to extend further into the lake.

Although sheltered shore-lines were not uncommon in valley lakes; the steeply sloping beds of these lakes prevented the development of wide bands of marginal vegetation. In the course of the survey it was noted that emergent vegetation did not grow in water deeper than 2 m, and in valley lakes water was sometimes 2 m deep only a few feet from the shore. Where shore-lines were exposed to wind, similar vegetation or the complete absence of it was noted in both valley and basin lakes.

The vegetation of the Wellington series was not exhaustively studied. The emergent vegetation varied according to the nature of the littoral area and the exposure to wind. In the shallow, sheltered basin lakes of the Horowhenua Plain emergent plants were abundant. Raupo (*Typha muelleri*) formed beds and was spreading lakewards in the shallow marginal waters. At Lakes Pukepuke and Kaikokopu a dense wide band of raupo completely surrounded the lakes, but at Lake Foxton No. 1 the dense growth was only on the eastern and southern shores. On the western shore of Lake Foxton No. 1 were scattered stands of sedges (*Scirpus, Cladium,* and *Eleocharis*). In Lakes Oturi and Brewer there were scattered stands of raupo, particularly on the western shore, and at Westmere of the sedges.

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* Introduced species.

In the valley lakes the emergent vegetation extended lakewards to the limiting depth of *c.* 1.5 m. Raupo formed a continuous though narrow band around Lakes Kopureherehe and Waitawa. At Lakes Westmere, Heaton, and Papaitonga scattered stands of raupo and sedges occurred. Raupo completely surrounded two islands in Lake Papaitonga. Lakes Waiau and Herengawe were exposed to the prevailing westerly winds, and the shores of these lakes sloped extremely steeply, while the eastern shores were wave-swept. In the shallower and more protected areas of the small bays stands of raupo and sedges were found.

The number of genera in the submerged vegetation was limited and species of *Potamogeton* and *Chara* were dominant. The floor of Lake Pukepuke was completely covered with these species. The submerged vegetation at Lakes Waitawa, Kopureherehe, and Foxton No. 1 was very sparse and consisted of a little *Chara*. The remaining lakes had only a slight density of vegetation, which consisted of scattered beds of *Chara* and *Potamogeton*. A small patch of *Ottelia ovalifolia* Rich.* was found at Lake Brewer, but at Lake Waiau there was an extensive bed completely covering the northern end of the lake. At Lakes Horowhenua and Pukepuke decaying *Potamogeton*, particularly, had been swept by waves into sheltered bays and then deposited in the shallows.

VII. Zoological Features

(*a*) *Invertebrate Fauna*

(i) *Plankton.*—The results for the qualitative collections for the Wellington series are given in Table 8, and for the quantitative collections for the Northland series in Table 7. The former are expressed as percentage by volume of the actual plankton, which is the volume obtained by allowing the suspension to settle in a graduated cylinder.

The samples for the Northland series were from pump collections and represent the "net plankton", as many organisms would have passed through the bolting silk, but where the plankton was rich this error would be reduced due to clogging of the net with the consequent retention of a larger portion of the plankton. The results for all collections are low except for Lake Kuwakatai.

(ii) *Bottom Fauna.*—The results of Petersen grab samples are given in Table 9. Mollusca, the dominant group, consisted mainly of species of *Potamopyrgus*, although in three lakes *Corneocyclas* spp. were associated with the *Potamopyrgus*. Nematoda and Diptera were the only other significant groups. The samples for three of the lakes developing a thermocline (Okaihau, Waitawa, and Kopureherehe) at the time of survey were particularly small. Lake Westmere, which also had a thermocline, had a much denser fauna than these three lakes.

The mean number of animals per sq. m. for the lakes was 1062, but the range was from 7 to 4990. Fuller and Cooper (1946), when studying

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* Introduced species.

TABLE 7

QUANTITATIVE PLANKTON RESULTS (HUNDREDS PER L.) FOR THE NORTHLAND SERIES

Lake	Total per l.	Phytoplankton																						Zooplankton		
		Dinobryon	*Staurastrum*	*Pediastrum*	*Oscillatoria*	*Scenedesmus*	*Cosmarium*	*Peridinium*	*Mougeotia*	*Botryococcus*	*Closterium*	*Ceratium*	*Pandorina*	*Eudorina*	*Nodularia*	*Trachylomonas*	Diatoms	*Diamorphococcus*	*Selenastrum*	*Xanthidium*	*Arthrodesmus*	*Actinastrum*	Rotifers	Nauplii	Copepoda	*Bosima*
Northland series																										
Waiparera	4,200	40						2																		
Ngatu	Nil																									
Rotokawau	T		T	T				T																		
Kanono	T																T									
Rototoa	T									T																
Kuwakatai	288,400	20	60	20	30	10	170	1560	70	540	10		50	130	10	20	100	10	20	T	T	T	10	10	4	
Kereta	T																									
Okaihau	Nil				T												T									
Pokoroa	15,700		7	1				127									14							1	T	T
Thompson's (*a*)	2,000							19				1														
(*b*)	2,500							24				1														
Muir's	10,800							84				24					T									
Wellington series																										
Kopureherehe	4,075	40														0.5							0.25			

T = Trace.

TABLE 8

PLANKTON RESULTS FOR WELLINGTON SERIES EXPRESSED AS PERCENTAGE BY VOLUME

																									Zooplankton											
			Phytoplankton																	Rotifera																
Lake	Mesh	Volume	Algal filaments	*Anabaena*	*Staurastrum*	*Pediastrum*	*Volvox*	*Spondylosium*	*Trichodesmium*	*Desmidium*	*Peridinium*	*Mougeotia*	*Botryococcus*	*Oedogonium*	*Ceratium*	*Asterionella*	*Eudorina*	*Trachylomonas*	Debris	*Keretella cochlearis*	*K. valga*	*Anuraeopsis fissa*	*Pompholyx camplanata*	*Asplancha*	*Filinia longiseta*	*Polyarthra trigla*	*Brachionus caudatus*	*Synchaeta*	*Pedalia mira*	*Trichocerca*	Nauplii	Cladocerans	Copepods	*Bosima*	Mysidacea	Amphipods
Oturi	150	2.0	T		T						40								50	T			T								T		T			
	60	1.5																	98														2			
Herengawe	150	1.0	50					T											45	1.5								1.5			T		T			
	60	1.5	T																40														60			
Waiau	150	1.5													25				70	T								T			T		T			
	60	1.5																	60	T																40
Okoia	150	1.0			T						T				T				60									T			T					
	60	1.5																	95												T		T			
Brewer's	150	17.0					75				15								10																	
	60	0.5			T						50				T			T	45												T			T		
Westmere	150	22.0							T						95					T		T	T				T				T		T			
	60	11.0													T																		95	T		
Pauri	150	6.0	45	T	20		T		5		20					T	T	T													T	T	T			
	60	35.0	T		T		50		T	T	T	T		T																		25	20			
Heaton	150	12.0	90			T	T						T							T			T	T	T				T	T	T		T	T		
	60	13.0					90																										10			
Foxton No. 1	150	1.0		T					T										50	40	T				T	T	T				T					
	60	1.0		T															50	40	T				T	T	T				T				T	
	60	4.0																	50														50		T	T
Papaitonga	150	2.0		T		T														60	T		T		T	T	30				2	T	T			
	60	1.0		T															55	T							T						40			

T = Trace.

TABLE 9

PETERSEN GRAB SAMPLES

Lake	No. of Samples	*Deleatidium* spp.	*Chironomus* spp.	Tabanid spp.	*Cyclorophorapha* spp.	Stick Caddis	*Oxythira* spp.	*Paracalliope* spp.	Mysids	Libelluloidea	Coenagrid	*Potamopyrgus* spp.	*Corneocyclas* spp.	*Planorbis* spp.	*Hyridella* spp.	*Isidora* spp.	Nematoda	Lepidoptera	Corixidae	Flatworms	Total Number	Mean	Animals per sq. m.
Northland series																							
Waiparera	1											3							1		4	4.0	95.2
Ngatu	2		1									2									3	1.5	35.3
Swan	2		4									12		1							17	8.5	201.0
Rotokawau	1		26																		26	26.0	617.0
Waingata	1		1														4				5	5.0	119.0
Kuwakatai	2		5									17					1				23	16.5	392.0
Okaihau	2		2																		2	1.0	23.8
Pokoroa	2		75										8		1		23				107	53.5	1272.0
Thompson's	2		2														28				30	15.0	356.0
Muir's	1		74				6					5					18		2		105	105.0	2499.0
Wellington series																							
Oturi	2		3									13			1	1	36	1			55	27.5	645.0
Herengawe	2		68	3				1	1			148	13				181	1	3		419	209.5	4990.0
Waiau	2		7	3			14		10	1		135	28		1	1	5			1	207	103.5	2460.0
Brewer's	1		1									5					1				7	7.0	166.7
Westmere	2	1	13								1	31	34	8			37		1		127	63.5	1520.0
Heaton	2		9			1						166	1	8	1		48		4		238	119.0	2830.0
Papaitonga	1	1	30									52	1	87			1	2			174	174.0	4145.0
Kopureherehe	3											1									1	0.3	7.1
Waitawa	3	1	3		1																5	1.6	38.0
Mean per sample	34																				1555		20172.1
Totals																						45.7	1062.0

the bottom fauna of the Maine Lakes, found that the mean value was about 300 animals per sq. m., and the range was from 200 to 475 per sq. m. They considered the fauna scant in these dune lakes, which were not noted for high productivity.

TABLE 10

CAPTURES OF INDIGENOUS AND INTRODUCED FISH

Lake	Designation	Indigenous Fish					Introduced Fish		
		Eels		*Galaxias* sp.	*Retropinna* sp.	*Gobiomorphus* sp.	Trout	Perch	Carp
		L.F.	S.F.						
Northland series									
Waiparera	1	—	L	P	—	P	—	—	—
Ngatu	2	—	—	P	—	—	—	—	—
Swan	3	L	D	P	—	—	—	—	—
Rotokawau	4	—	—	P	—	—	—	—	—
Waingata	5	—	—	P	—	—	—	—	—
Kanono	6	—	—	P	—	P	—	—	—
Rototoa	7	—	—	P	—	P	—	—	R
Kuwakatai	8	—	—	—	—	P	—	—	—
Kereta	9	—	—	—	—	—	—	—	—
Okaihau	10	—	—	—	—	P	—	—	—
Pokoroa	11	L	D	P	P	P	—	—	—
Thompson's	12	L	—	—	—	P	—	—	—
Muir's	13	D	D	—	P	P	—	—	—
Wellington series									
Oturi	14	—	S	—	P	P	R	—	P
Herengawe	15	S	—	—	P	—	—	—	—
Waiau	16	L	S	—	—	—	—	R	R
Okoia	17	S	—	—	—	—	—	—	—
Brewer's	18	—	—	—	—	P	—	P	P
Westmere	19	L	D	P	—	—	—	P	—
Pauri	20	L	L	—	—	—	P	P	—
Heaton	21	S	L	—	P	P	—	—	—
Bernard	22	L	S	—	—	—	—	—	P
Pukepuke	23	L	L	—	P	—	—	P	—
Foxton No. 1	24	D	D	—	P	P	P	P	—
Horowhenua	25	L	S	—	—	P	R	—	P
Papaitonga	26	S	L	—	—	P	—	—	P
Kopureherehe	27	S	S	—	—	P	R	—	—
Waitawa	28	L	D	P	P	P	—	—	—

Eels: S = one or two caught; L = 3-10 caught; D = above 10 caught.
Fish: P = present; R = reported, but not verified.

Muttkowski (1918) studied the density of the bottom fauna of Lake Mendota intensively in relation to depth. His figures show an increase from 850 per sq. m. at 0.1 m to 2530 at 3-5 m, with a decrease to 1190 at 5-7 m. The mean was 1336 animals per sq. m. Lake Mendota has a good bottom fauna.

In Lakes Okaihau, Ngatu, Waitawa, and Kopureherehe the fauna was sparse, and in the remainder scant to good.

Dredge samples consisted mainly of species of *Potamopyrgus* and some *Corneocyclas.* It was noticeable that in Lakes Westmere, Kopureherehe, and Waitawa the bulk consisted of large numbers of empty shells from the above species, and very few molluscs were alive at the time of collection. It is possible that these collections were made in the shell area.

TABLE 11

METHOD OF CAPTURE OF EELS

Lake	Short-finned			Long-finned		
	Fyke	Pot	Seine	Fyke	Pot	Seine
Northland series						
Waiparera	1	—	—	—	—	—
Swan	31	—	—	3	—	—
Pokoroa	66	1	6	6	—	—
Thompson's	—	—	—	1	5	—
Muir's	57	12	—	2	24	—
Wellington series						
Oturi	2	—	—	—	—	—
Herengawe	—	—	—	1	1	—
Waiau	1	—	5 (gaff)	—	3	—
Okoia	—	—	—	—	1	—
Westmere	—	28	—	—	6	—
Pauri	—	—	1	1	—	—
Heaton	1	—	3 (1 gaff)	—	1	—
Bernard	—	—	2	—	6	—
Pukepuke	—	3	—	—	7	—
Foxton No. 1	4	4	52	—	15	—
Horowhenua	1	—	—	—	7	—
Papaitonga	—	3	1 (gaff)	—	2	—
Kopureherehe	1	—	—	—	—	—
Waitawa	4	5	36 (14 gaff)	1	5	1

The freshwater mussel (*Hyridella* spp.) was widespread and was probably present in all the lakes. Often, for example in Lakes Kopureherehe and Waitawa, parts of decomposing shells were obtained in grab and dredge samples, even though no specimens of live animals were found. In Lake Kereta a particularly extensive bed was noted, and large numbers were also dredged from Lakes Waiau and Herengawe.

The freshwater crayfish (*Paranenphrops planifrons* White) appeared to be more widespread in the Northland series, being particularly abundant in the lakes near the Kaipara Harbour. Large numbers were taken in the Wanganui lakes of the Wellington series. They had a widespread distribution and were probably present in all lakes.

Dragonflies were hatching during the survey of the Northland lakes and adults of the groups Aeschnidae and Libellulidae were taken. They were particularly common on north and south heads of Kaipara Harbour.

(*b*) *Vertebrate Fauna*

As the intensity of fishing effort varied considerably from lake to lake, often it was only possible to verify the presence or absence of various species. Occurrences of introduced and native fish are given in Table 10.

TABLE 12

TROUT LIBERATIONS IN THE WANGANUI LAKES

Date	Age	Size	Number
Lake Kowhata			
Rainbow			
Apr. 1948	Fingerlings	3-5 in.	11,900
June 1948	Fingerlings	3-5 in.	
June 1948	Yearlings	10 in.	100
Sept. 1949	Fingerlings	3-5 in.	4,900
Sept. 1949	Yearlings	10 in.	100
Apr. 1950	Fingerlings	3-6 in.	5,300
Brown			
Sept. 1949	Yearlings	12 in.	25
Lake Pauri			
Rainbow			
Apr. 1948	Fingerlings	3-5 in.	5,000

(i) *Indigenous Fish*

(1) *Eels.*—Long-finned (*Anguilla dieffenbachii* Gray) and short-finned (*A. australis schmidtii* Phillipps) eels were taken from all lakes with a temporary or permanent outlet. Lake Brewer was the only eel-free lake of the Wellington series. Only Lakes Waiparera, Swan, Pokoroa, Thompson's, and Muir's of the Northland series contained eels. From some waters large numbers of eels were taken and Table 11 shows that short-finned eels were usually taken by seining or by fyke nets, whereas the long-finned eels were trapped. At Lake Waiparera an unusually large short-finned eel 3 ft 4 in. long and weighing 7 lb 14 oz was taken.

(2) *Other Native Fishes.*—Various species of *Galaxias, Gobiomorphus,* and *Retropinna* were recorded. Mullet (*Mugil cephalus* L.) were present in Lake Pokoroa and also in Lake Kaikokopu of the Wellington series. At Lake Pokoroa infrequent fishing for mullet takes place and the team caught a 19-in. fish weighing 3½ lb.

(ii) *Introduced Fish*

No spawning grounds are available for trout in any of these lakes. Good stocks of rainbow trout are maintained in some lakes by artificial liberations. Fry are normally liberated, although sometimes yearling fish have been released. Rainbow fry have been liberated in most lakes with little success, except that a few fish may have persisted for some years. Table 12 lists the liberations in two lakes having established trout stocks.

(1) *Brown Trout.*—Brown trout were recorded only at Lake Foxton No. 1 where two 12-in. fish were caught. Brown trout have been reported in Lake Horowhenua, and the Wellington Acclimatization Society reports fish up to 14 lb having been taken.

TABLE 13

RAINBOW TROUT FROM LAKE KOWHATA, MAY 1950

Length (in.)	Weight lb	oz	Condition Factor	Sex	Age
16.00	1	7.5	36	Female	3
11.75	0	9.0	35	Female	2
11.00	0	6.0	28	—	1
9.75	0	4.8	33	—	1
9.00	0	3.5	31	Male	2
10.50	0	4.0	22	Female	2

(2) *Rainbow Trout.*—No rainbow trout were caught although their presence at Lakes Alice, Pauri, and Kowhata was verified. The Wanganui Acclimatization Society had made several liberations of fish in Lakes Kowhata and Pauri, as shown in Table 12. No detailed catch data, however, were available for these lakes, but measurements made on a sample of fish in May 1950 are given in Table 13. The condition factor of these fish is particularly low and this may be due to the initial excessive liberations made. The Wellington Acclimatization Society has for many years maintained a stock of rainbow at Guddop's Lake by artificial liberations, mainly of fingerlings. Unfortunately no details of liberations were available. Catch return data extracted from angling diary returns are shown in Table 14. It is noticeable that the size of fish caught was comparable with stream fish and that in the 1950-51 season, particularly, the fish were large, although the rate of catch was low.

TABLE 14

CATCH DATA FOR GUDDOP'S LAKE

Season	Time Fishing (days)	Time Fishing (hr)	Under-sized Fish	Over-sized Returned	Kept	Mean Length (in.)	Fish per Hr
1948-49	1.5	13.5	—	1	10	14.6	0.82
1949-50	3.0	20.5	—	—	11	12.7	0.82
1950-51	5.0	38.0	—	—	11	16.0	0.29

(3) *Perch.*—Perch were caught in five lakes, but they are known to be present in some other lakes not surveyed. They were reported to be present in Lake Herengawe, but this was not verified. No perch were

caught in the Northland series but they are known to be present at Glink's Gulley on north Kaipara Harbour. Details of the perch caught are given in Table 15. In 1896 the Wellington Acclimatization Society reported that a further 44 perch were liberated in Lake Waitawa, and 24 in Lake Kopureherehe. No data are available about their survival and no perch were caught when these lakes were surveyed.

(4) *Carp.*—*Carassius* spp. were taken at Brewer's Lake and at Lake Heaton. They have been liberated in Lake Rototoa, but their presence was not verified.

TABLE 15

METHOD OF CAPTURE AND LENGTH OF PERCH

Lake	Method of Capture	Number Caught	No. Weighed and Measured	Mean Length (in.)	Range in Length (in.)
Foxton No. 1	Gilled	41	14	13.0	12.00-14.50
Foxton No. 1	Seined	6	6	12.8	4.00-14.00
Pukepuke	Gilled	17	17	10.9	9.00-12.50
Westmere	Gilled	10	4	11.3	10.00-12.50
Nowell	Trolling	9	9	9.3	5.75-12.75
Pauri	Seined	2-300	—	All < 9	<9

(5) *Gambusia.*—*Gambusia affinis* Baird & Girard were recorded at Lake Ngatu only, where they had been introduced specifically for mosquito control.

(iii) *Waterfowl*

An intensive study of the waterfowl was not made, but their presence was recorded.

(1) *Grey Duck.*—*Anas poicilorhyncha* Gmelin was of wide distribution and abundant in the Himitangi area. Large numbers were present at Lakes Pukepuke and Kaikokopu. They were also present at Lakes Pauri, Waitawa, and Westmere. About 15 greys were seen at Lakes Okaihau, Kereta, and Kuwakatai, and they were present at Lakes Pokoroa and Rotokawau.

(2) *Mallard Ducks.*—No mallard ducks (*A. platyrhynchus* L.) were seen but they are sometimes present at Lakes Waitawa, Kopureherehe, Pukepuke, and Kaikokopu.

(3) *Black Swan.*—Five black swans (*Chenopis atrata* Latham) and two cygnets were seen at Lake Pukepuke and there were large numbers at Lake Kaikokopu. At Lake Kereta approximately 30 adults and two cygnets were seen. Black swans were also present at Lake Pokoroa.

(4) *Stilts.*—Two pied stilts (*Himantopus* sp.) were seen at Lake Pukepuke and one at Lake Waingata. Six stilts were observed at Lake Rotokawau and at Lake Kereta.

(5) *Shags.*—*Phalacrocorax* spp. were seen at Lakes Pauri, Pukepuke, and Foxton No. 1. They were probably all black shags (*P. carbo* L.). Black

shags were also plentiful at Lakes Waitawa and Kopureherehe, where at least 25 were seen. There was a rookery in the trees on the edge of Lake Waitawa. A black shag was shot at Lake Brewer.

Little pied shags (*P. brevirostris* Gould) were seen at Lakes Okaihau, Pokoroa, Kuwakatai, Rototoa, and Rotokawau. A little black shag (*P. salcirostris* Branto) was seen at Lake Kuwakatai.

(6) *Kingfisher.*—One (*Halcyon vagans* L.) was seen at Lake Bernard and kingfishers were present at Lake Okaihau. Two were heard only at Lake Pokoroa and at Lake Rototoa.

(7) *Bittern.*—No bitterns (*Botaurus poiciloptilus* Wagler) were seen on the Wellington series, but they are known to be present at the Foxton lakes and Lake Kaikokopu. In Northland they were seen at Lakes Thompson, Swan, and Rototoa.

(8) *Grebe.*—The little grebe, or New Zealand dabchick (*Podiceps* (*Poliociphalus*) *rufopectus* Wagler) was found at Lakes Pokoroa, Kereta, and Kanono.

(9) *Pukeko.*—*Porphyrio melanotus* Temminck was seen at Lake Kopureherehe, and at Lake Kuwakatai 15 birds were noted.

VIII. DISCUSSION

The suitability of lakes for game fish may be considered from several points of view:

(*a*) *Wind and Wave Action*

Wind and wave action are important features of lake physiology as the surface waters of a lake are hardly ever calm. The height of waves is proportional to the pressure of the wind on the lake surface and to the distance travelled (Muttkowski 1918). The lakes of the Northland and Wellington series are exposed to the prevailing winds and few are so sheltered as to be not affected by the winds. The effects of wind and wave action may be discussed under several headings:

(i) *Shore-lines*

(1) *Erosion.*—Shore-line modification by erosion is very important and the eastern shore-lines of the larger lakes surveyed, particularly of the Northland series, are being rapidly eroded. At Lakes Kanono and Rototoa the eastern shore consists of cliffs and small stacks. Remnants of stacks are also found in shallow water on the wave-cut platform, which is of varying width extending from these cliffs and slopes steeply into deep water. There is little or no accumulation of debris on these shores as it is carried directly into deep-water bays or the entrances of bays, where the backwash is less (Pearsall 1917).

A dominant feature of such a shore-line is the barrenness. Few (if any) submerged or emergent aquatic plants can grow and bottom fauna is sparse, owing to the unstable and shifting nature of the bottom.

Wave-cut platforms and sandy beaches are comparable for the small numbers of bottom fauna supported, again owing to the continual shifting of the sand and fine deposits, enabling only the slow colonization by plants and associated bottom fauna.

(2) *Sand Deposition.*—The modern moving dunes of the foreshore are encroaching from the west. Freely running sands are common on the western shores of many of the lakes, particularly those of Northland. Lakes Kanono, Kuwakatai, and Rototoa all have advancing dunes. Cockayne (1911) drew attention to the destructive effect of drifting sands upon lakes and lagoons. According to local information a small lake at Waihopai Stream, north head, Kaipara Harbour, has been completely overwhelmed by drifting sand. In its place there is a flat expanse of sand on which the only indication of swamp conditions is a patch of raupo growing in one corner. Although some of the lakes are being slowly filled in by drifting sand, they are of sufficient size and depth to support a game fishery for some years before being completely filled.

Shore-lines with freely running sand are also barren, as no littoral area is developed and the shore slopes steeply to the lake bed. The rate of deposition of sand usually exceeds the rate of colonization by aquatic plants.

(3) *Marginal Plants.*—In the sheltered areas of the shallower basin lakes, where emergent vegetation is extending lakewards because of reduced wave action, the deposition of silt and decaying plant material is enhanced. This deposition of debris, the development of plant communities, and the formation of peat deposits were noticeable at Lakes Muir, Pokoroa, and Swan. The development of such marginal areas is aiding dystrophy in these waters.

(4) *Submerged Aquatic Plants.*—The submerged plant species may be dislodged, particularly at the end of the active growing season, by wave action. In shallow water they may also be dislodged by feeding aquatic waterfowl. The debris may be swept towards deeper water by the backwash and deposited, or in shallower lakes may be moved across the lake by wind and wave action and be re-deposited in the shallows. Deposits of recently dislodged dead and decaying species of *Potamogeton* were noted in Lakes Horowhenua and Pukepuke. Where this debris becomes entangled in stands of emergent vegetation, on decay it provides further plant nutrients.

(ii) *Water Turnover*

(1) *Temperature.*—In the summer under still conditions the surface waters heat rapidly and thermal stratification may be established. The maximum surface temperature was 24°C. This may not be high enough for the spawning requirements of plant-spawning species. In these lakes, however, wind plays an important part in preventing this stratification and stagnation. The waters of Lakes Rototoa and Kuwakatai, which are

well exposed to westerly winds, are turned over to a depth of 10 m. Stratification does occur in the sheltered lakes for long periods, and may, for short periods only, be developed even in the large and exposed lakes, and occur more commonly than was found in the survey. It appeared as though a thermocline had been destroyed by wind in Lake Rototoa. Within the Wellington series water turnover was complete in most lakes.

(2) *Dissolved Substances.*—Waters of the exposed lakes are well oxygenated, but oxygen is lacking in the deeper waters where stratification is maintained for some time. There always appears to be adequate oxygen, with the exception of the hypolimnion in stratified lakes. Currents and wind action distribute essential chemicals throughout the lake volume and decomposition products from the lake bed are also distributed and eliminated from the surface waters quickly. Gassing (probably methane) was noted in one instance only in the shallow stagnant arm of Lake Kuwakatai.

Inorganic substances, although present in small concentrations, appear adequate to support game fish.

(3) *Organic Matter.*—From visual observation on the lake waters and quality of plankton samples there appeared to be a much higher concentration of organic matter in the Palmerston North-Otaki lakes of the Wellington series and Lakes Westmere, Swan, Okaihau, Muir, Pokoroa, and Thompson. In the mesotrophic lakes of the Northland series little organic material seemed to be present. Dissolved and suspended organic matter was not measured.

(4) *Transparency.*—Sufficient light appears to penetrate even the most eutrophic lakes, for even these support dense growths of aquatic plants.

(5) *Productive Volume.*—The lake form and slope determine the relative amount of shallow water. The biological productivity is greater the more the superimposition of the photosynthetic and decomposition zones. The photosynthetic zone may be considered the littoral area where emergent and submerged plants are actively growing, and the decomposition zone is where this plant debris decays. A close superimposition of these zones occurs in protected shallows where the bottom slope is small, permitting active plant growth and the accumulation of organic deposits. This leads to a more diversified flora and fauna.

The valley lakes, particularly of the Northland series, have steeply sloping sides and there is little shallow water for the development of a littoral zone. Debris is swept to the depths where it is not immediately available for use by plants and animals. Lake Rototoa and Kuwakatai are examples and, in these, only isolated patches of emergent plants are found on the western shores. The valley lakes of the Wellington series are much shallower and the whole of the lake bed may be in the littoral zone.

IX. ANGLING POTENTIAL

Access to most of the dune lakes is fairly easy from roads across rolling country, and it appears that only three private waters were surveyed. A private water, as defined in the Fisheries Act (1908) "means any waters wholly contained within the land of one private owner, but does not include the waters of a permanent river or stream, or lake which passes or extends from the land of one owner to that of another, nor any water not wholly contained within the land of one private owner." It appears that Lakes Brewer, Rotokawau, and Waingata come within this category.

(*a*) *Present*

Some lakes are at present stocked with trout or perch. The lakes stocked with trout support moderate angling, and the stocks are normally maintained by liberation of fry, with occasional releases of yearling fish. Some of the lakes having self-supporting perch stocks could probably carry a greater intensity of angling, as some are hardly fished. It is well known to anglers that although perch cannot be considered in the same class as trout as a fighter, it is considered a far better table fish. The capture of takeable-sized perch (size limit now 6 in.) in the Wellington series even surprised the local inhabitants. It may be that anglers are not aware of the existence of some of these stocks of perch.

(*b*) *Future*

The length of shore-line fishable varies considerably at each lake, but is normally only a small part of the total length. Tall land plants and broad belts of emergent plants prevent access to the water. Wading along the edge of these banks is not practicable because the depth of water is 1-1½ m, with a slippery clay bed often steeply sloping to the deeper water. Northland lakes have less emergent vegetation, but the lake sides are fairly steep and may even consist of large areas of running sand or slippery wave-cut platforms.

The biological survey was not detailed enough or of sufficient duration fully to measure the potential of these lakes for fishing. More detailed studies of a limited number of waters for a period of about a year will be necessary before the selection of a new game fish can be made.

X. ACKNOWLEDGMENTS

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APPENDIX I

The values for oxygen concentration in both the Wellington and Northland series of lakes were determined by the unmodified Winkler method.

Roberts, Grindley, and Williams (1940) state, "There is abundant proof that the preliminary oxidation of the sample is necessary before conducting the test (for oxygen)". Four samples of Wellington tap water were analysed in October 1951; two samples by the unmodified Winkler, and two using the oxidation modification as described by Roberts, Grindley, and Williams. The results are given in Table 16.

TABLE 16

OXYGEN IN WELLINGTON TAP WATER, OCTOBER 29, 1951

Oxygen (ml/l)	(Winkler)	Oxygen (ml/l)	(Modified Winkler)
6.265	6.296	6.044	6.047

It will be seen that results for each pair of samples are comparable and that the analysis by the modified method gives the better comparative figures. There is a slight discrepancy between the methods.

A series of field tests was carried out in the Upper Karori Reservoir, Wellington (Stevenson 1952) on November 10 and 11, 1951. The reservoir is a eutrophic one and the water has a high organic content. Four series of samples throughout a 24-hr period were taken at various depths and the analysis for oxygen was made by the unmodified Winkler and modified Winkler methods. The samples for these analyses were collected in the water sampler used on the Northland series, and the bottles were filled without bubbling. A typical series of results (taken at 3 m) is given in Table 17.

It is noticeable that there is a wide difference between the oxygen values determined by both methods.

The oxygen saturation values are unusually high for the Wellington series of lakes. As these samples were analysed by the standard Winkler method and as most of the lake waters have a high organic content, a further series of oxygen determinations was made at Lakes Waitawa and Kopureherehe on August 26, 1952. Oxygen determinations were made by the normal and modified Winkler methods. The samples were taken in the spring after a warm, calm period of about a week. In Lake Waitawa the Secchi disc reading was 1.5 m for a 1-dm disc. The water samples were collected in a modified displacement sampler after Roberts, Grindley, and Williams (1940). Water temperatures were taken by direct measurement of the water in the sampler. Table 18 gives the values for oxygen by both methods and the percentage saturation figures.

The results of this analysis agree with those from the Karori Reservoir as there is a marked discrepancy between oxygen content determined by the Winkler and modified Winkler methods.

TABLE 17

OXYGEN DETERMINATIONS (ML/L) AT THE UPPER KARORI RESERVOIR

Time	a.m.	p.m.						a.m.				
	10.30	12.30	2.30	4.30	6.30	8.30	10.30	12.30	2.30	4.30	6.30	8.30
Oxygen (Winkler)	7.7	7.6	7.4	7.6	7.2	6.0	7.6	7.5	7.0	7.3	7.7	7.1
Oxygen (modified Winkler)	4.8	4.5	5.3	4.7	5.4	4.4	1.8	4.4	5.2	4.1	4.2	3.7

The percentage saturation values of the surface samples at Lakes Waitawa and Kopureherehe are 73 and 98 by the unmodified Winkler, and 52 and 65 by the modified Winkler methods respectively. The percentage saturation values for the original survey (for midsummer) for surface samples were at Lake Waitawa 152, and Lake Kopureherehe 110 (Table 2). These values were very high and the lake waters probably were not supersaturated to this high degree. It is probable that the

TABLE 18

OXYGEN DETERMINATIONS AT LAKES WAITAWA AND KOPUREHEREHE

	Lake Waitawa				Lake Kopureherehe					
Depth (m)	0	2	4	5	0	2	4	6	8	10
Temperature (°C)	11.50	10.50	10.00	10.00	12.50	10.50	9.75	9.50	9.50	9.25
Oxygen (Winkler) (ml/l)	5.61	4.50	4.42	3.80	7.31	5.59	6.13	6.10	5.03	5.97
Saturation (Winkler) (%)	73	58	55	48	98	75	77	76	63	74
Oxygen (modified Winkler) (ml/l)	3.90	3.76	3.10	2.52	4.89	4.48	3.24	4.23	3.91	3.29
Saturation (modified Winkler) (%)	52	49	40	30	65	58	40	53	49	40

results for the Wellington series are high and may have been affected, particularly at Lakes Waitawa, Kopureherehe, Papaitonga, Pukepuke, and Horowhenua, by organic matter present as no check was made on pH during alkalization. This may also have been true for Lakes Muir, Thompson, Pokoroa, and Okaihau of the Northland series. The results have suggested that further examination is desirable as the inorganic analysis was incomplete. Organic matter may affect the dissolved oxygen content, but inorganic radicals may cause much greater effects and mask those of the organic matter. The preliminary oxidation, therefore, may have been detrimental rather than beneficial. Further analyses to elucidate this problem are being planned.

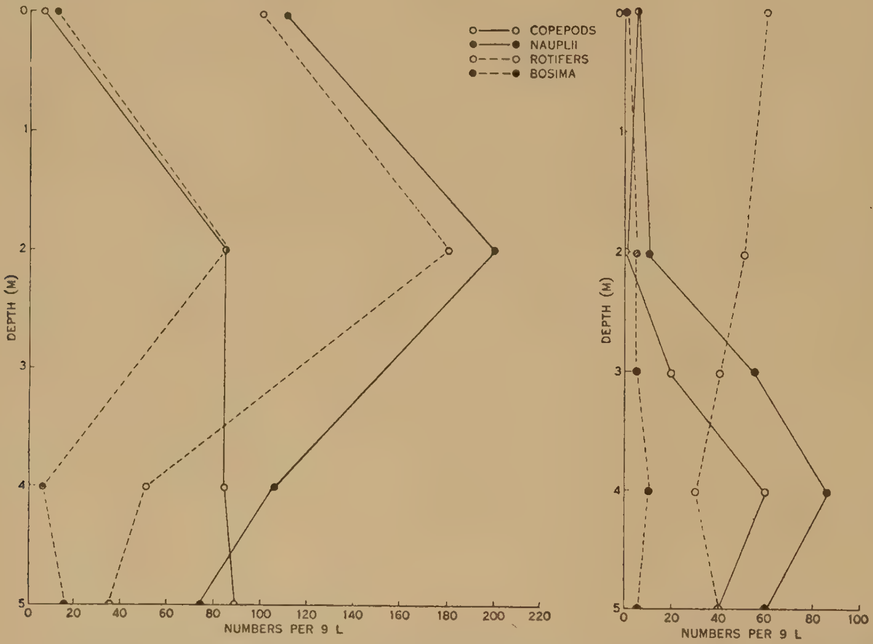


Fig. 12.—Organisms in relation to depth at Lakes Kopureherehe (left) and Waitawa (right).

Appendix II

Also on August 26, 1952, further plankton collections were made at Lakes Waitawa and Kopureherehe.

(*a*) *Lake Kopureherehe*

(i) *Total Plankton.*—The total plankton of the surface water was found by a combination of the Sedwick-Rafter method of sand filtration and centrifuging of the concentrate, the plankton of 1 l. of water being concentrated to 0.5 ml. A portion of this was then counted in a haemacytometer cell. The chamber used was made deeper than that used for blood counting. With organisms present in large numbers a portion was examined equivalent to 4 ml of the original water. With organisms present in small numbers a portion equivalent to 10 or 50 ml was counted, depending on the number present.

Diatoms	*Cyclotella*	216,000
	Others (predom. *Navicula*)	21,000
Staurastrum spp.		13,000
Ankistrodesmus		8,000
Peridinium		150
Eudorina		30
Closterium		20
Oocystis		20
Total		258,220 per l.

(ii) *Surface Tow.*—A surface haul was made using a net 196 meshes per in. Zooplankton formed about 70 per cent. of the volume, this being predominantly rotifers, with Nauplii also present. The phytoplankton was predominantly *Eudorina, Staurastrum,* and *Peridinium,* with *Tabellaria, Closterium, Mougeotia, Phormidium,* and *Polycystis* present.

(iii) *Plankton Pump Samples.*—The samples were obtained by passing 9 l. (2 gal) through 100-mesh bolting silk. One-fifth of each sample was examined and the figures quoted represent the total per 9 l. Only the zooplankton was considered. Even with zooplankton it was only the copepods and *Bosima* that would with certainty be retained on the silk; some of the rotifers and nauplii, because of their small size, would have certainly passed through. No definite conclusions could be drawn from a single sampling.

(*b*) *Lake Waitawa*

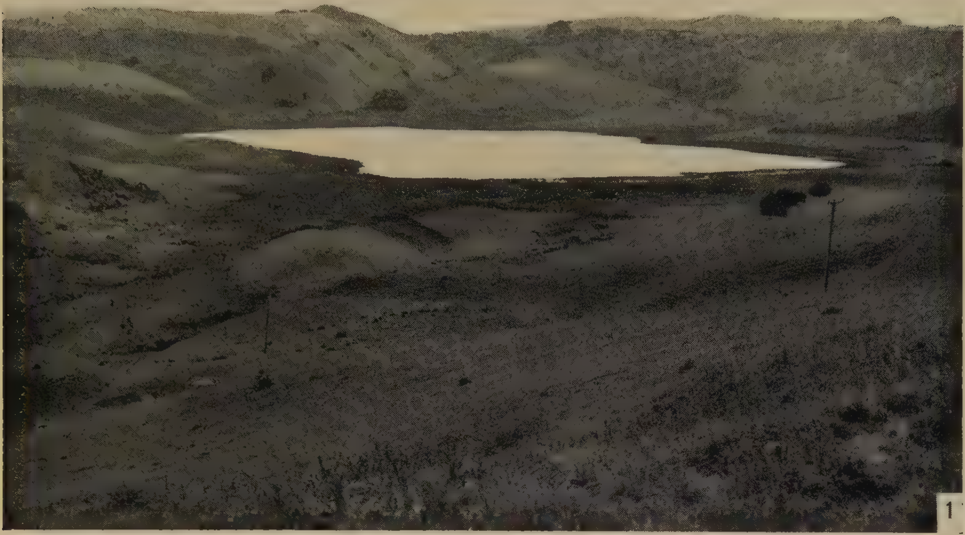
(i) *Total Plankton.*—The total plankton of the surface water at Lake Waitawa was:

Closterium	440,000
Trachylomonas	131,000
Peridinium	20,000
Dictyosphaerium	38,000
Stephanodiscus	38,000
Ankistrodesmus	128,000
Actinastrum	5,000
Ciliates	5,000
Misc. diatoms	100
Rotifers	320
Eudorina	50
Nauplii	40
Ceratium	20
Anabaena	20
Total	805,550 per l.

(ii) *Surface Tow.*—Zooplankton approximately 60 per cent. of volume, this being predominantly rotifers and nauplii, with copepods and *Bosima* present. Phytoplankton predominantly *Peridinium* and *Closterium,* with *Ceratium, Trachylomonas, Dictyosphaerium, Actinastrum, Ankistrodesmus, Staurastrum,* and *Eudorina* present.

(iii) *Plankton Pump Samples.*—Pump samples were also taken. Figure 12 shows the distribution of the zooplankton against depth for Lakes Waitawa and Kopureherehe.

COASTAL DUNE LAKES IN NEW ZEALAND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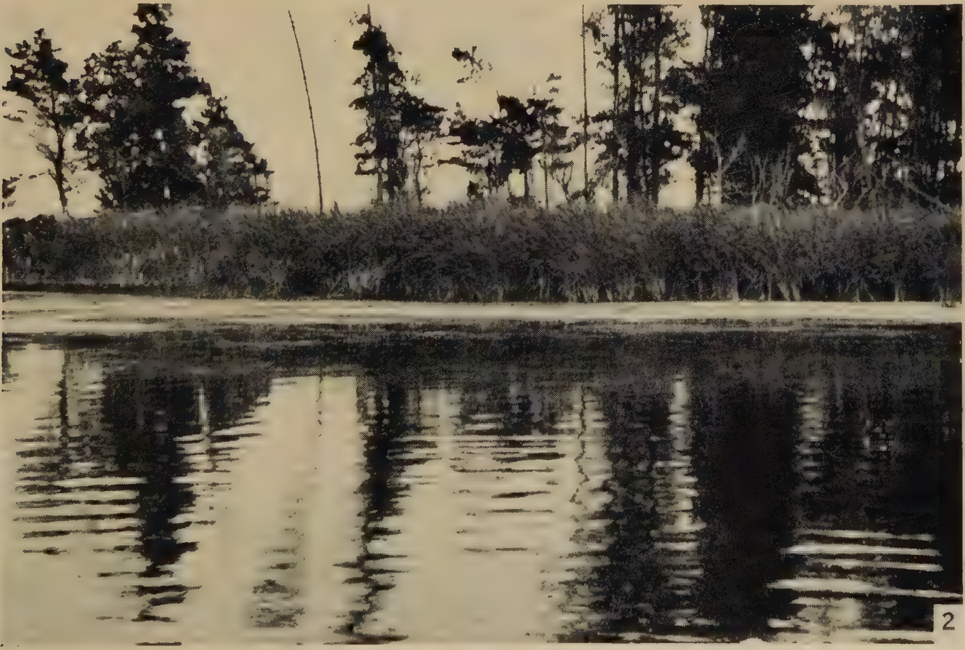
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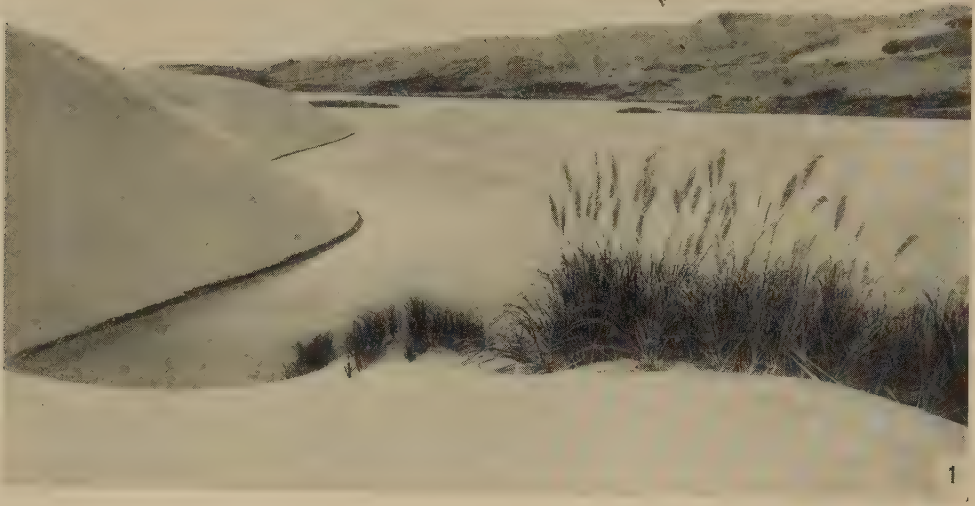
Fig. 1.—Lake Pokoroa. A typical basin lake in consolidated dunes. (Photo: B. T. Cunningham.)

Fig. 2.—Lake Kaikokopu. A shallow lake of the Wellington series, showing the dense band of raupo (*Typha muelleri*) which surrounds many lakes. The bed was about 5 yd wide. (Photo: B. T. Cunningham.)



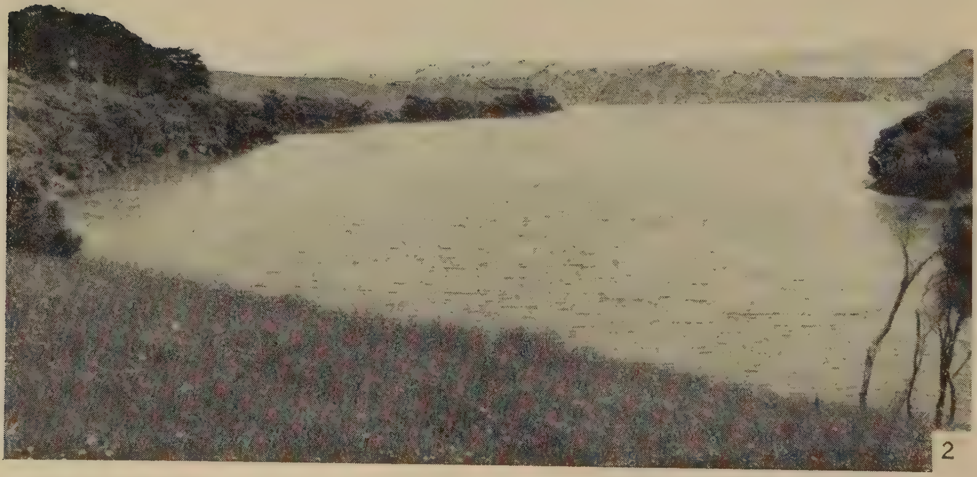


Fig. 1.—Lake Kereta. Moving sand on the western shore and old consolidated dunes on the eastern shore (Photo: A. W. Torrie.)

Fig. 2.—Lake Rototoa. A typical valley lake in Northland. In the distance recently stabilized dunes and moving sand can be seen. (Photo: B. T. Cunningham.)

MODIFIED WHIRLING APPARATUS FOR THE SUBSAMPLING OF PLANKTON

By PATRICIA KOTT*

(*Manuscript received April* 27, 1953)

Summary

An apparatus for the subsampling of plankton is described. It is shown that the samples obtained conform to the characteristics of a Poisson distribution. Limits to the efficiency of the apparatus are encountered when certain organisms with a tendency to clump together are present in high concentrations, but these limits are well within the accuracy required and achieved with the present methods of collecting plankton; otherwise the accuracy of the apparatus apparently does not vary with different types of organism.

I. INTRODUCTION

The apparatus is a whirling vessel, based on the principle of that originally designed by Lea and Rollefsen at the Fisheries Directorate, Bergen, about 1930, and later modified and described by Wiborg (1951).

The advantages of the present modifications are achieved by a reduction of the apparatus to the simplest possible form; a reduction in the height of the compartment sectors so that turbulence in the system is effective and the sectors do not form a barrier to mixing of the larger and heavier organisms; and use of an open "Perspex" or glass vessel so that visual appraisal of the subsamples is possible and washing and general handling of the apparatus are facilitated.

II. DESCRIPTION

The vessel (Plate 1, Figs. 1 and 2) is made of "Perspex" and is 14.5 cm in diameter and 7 cm deep. The top is completely open, and the base is divided into 10 compartments by strips of "Perspex" 1.2 cm wide at the base, but sloping to a width of 0.3 mm at 0.7 mm from the base. The sectors then continue vertically for 0.3 mm, and are thus 1 cm high.

Centrally there is an 80 mesh/in. gauze cylinder (Plate 1, Fig. 3), 4 cm in diameter and 4 cm high. It is strengthened by a solid brass band around the base covering the gauze to about half the height of the sectors. Brass strips corresponding to the inner ends of the sectors continue from the base to the surface of the cylinder, and then are continuous with a solid brass plate which covers the top of the cylinder, leaving the gauze exposed in the centre only. Beneath this cylinder is a hole in the base of the apparatus which is continuous with a tube passing down and opening below the turntable on which the whole apparatus is mounted. The turntable (Plate 1, Fig. 4) supports the vessel on a metal plate of the same diameter, and it revolves by means of a hollow cylinder (through

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which the central outlet tube of the "Perspex" vessel passes) on a similar basal plate mounted on legs.

III. USE OF THE APPARATUS

The central tube is corked and the plankton sample poured into the cylinder. Care is taken to see that the fluid is at least 3 mm above the top of the sectors. The vessel is then rotated rapidly by hand and stopped suddenly; this process is repeated four or five times. The turntable is so constructed that there is movement only in the horizontal plane. The cork is then removed from the outlet tube and the fluid drained from the sample until the level is just below the top of the sectors. It is sometimes necessary to revolve the vessel again during this draining operation, as the plankton tends to clog the gauze; it is thrown off when the vessel is rotated. When sufficient fluid is drained off the cork is replaced in the outlet tube and samples may be removed from the sections with a pipette. This is extremely efficient since, as the sample is removed from the compartment, fluid drains in from the central cylinder and clears the gauze of any organisms adhering to it. More fluid may be added when the sample is rich to achieve complete washing of the compartment. It was found necessary to leave the gauze of the central cylinders uncovered to half the height of the sectors since the liquid is held against it in a high meniscus, and only by having the gauze considerably lower than the level required is any continuity of fluid across the top of the sectors removed.

TABLE 1

DIMENSIONS OF COMPARTMENTS

Compartment	Outer Chord (cm)	Inner Chord (cm)
1	4.05	0.99
2	4.18	1.04
3	4.15	0.80
4	3.95	1.00
5	4.10	1.05
6	3.98	0.94
7	4.26	1.04
8	4.33	1.05
9	4.13	1.05
10	4.14	1.05

IV. RESULTS

There are slight differences in the dimensions of the compartments in the particular instrument tested; measurements for the upper surface are set out in Table 1.

For three hauls, the organisms in each of the 10 compartments were counted, and the counts are set out in Table 2. Analyses of variance were carried out for individual organisms and for the total count in each compartment in each haul, but on no occasion was any significant between-compartment difference demonstrated. The 10 total compartment counts for each haul were also ranked in order and compared with the ranking

TABLE 2

NUMBER OF ORGANISMS FROM EACH COMPARTMENT

Compartment	Fish Larvae	Fish Eggs	*Oikopleura*	*Fritillaria*	Decapod Larvae	*Evadne tergestina*	*Penilia smackeri*	Copepods	Chaetognaths
				Haul I					
1	—	—	16	16	3	7	184	1200	14
2	3	—	17	27	4	7	192	1195	28
3	1	—	17	17	9	7	206	1260	28
4	1	—	20	22	13	13	214	1315	28
5	—	—	24	22	11	14	210	1315	33
6	3	—	26	15	6	18	216	1330	34
7	—	1	27	20	7	12	208	1160	32
8	3	—	26	14	7	17	206	1200	24
9	2	2	22	20	6	14	200	1100	33
10	2	1	27	25	6	8	212	1225	26
				Haul II					
1	2	—	24	19	5	9	190	1400*	31
2	2	1	19	14	8	10	224	1400	30
3	1	1	20	15	5	11	212	1450	27
4	1	2	18	14	9	24	236	1450	34
5	1	2	28	15	7	18	216	1450	28
6	2	2	25	19	7	17	250	1450	28
7	1	—	28	25	6	15	230	1500	43
8	2	—	28	16	8	24	232	1500	42
9	1	1	26	19	6	17	258	1450	34
10	2	2	30	15	8	20	200	1400	25
				Haul III					
1	—	5	5	1	—	20	66	580	10
2	—	4	3	2	—	20	116	618	13
3	—	5	3	2	—	18	80	610	9
4	—	4	4	2	—	19	80	550	6
5	—	3	3	4	—	28	102	630	5
6	—	2	5	2	—	20	90	625	7
7	—	1	3	—	—	15	76	620	8
8	—	5	11	2	—	17	116	650	14
9	—	5	2	4	—	21	110	665	9
10	—	3	6	5	—	18	82	640	13

* This series counted to the nearest 50.

of the compartments on size, but again no consistency could be demonstrated. The differences in size between compartments cannot therefore be regarded as exerting any significant effect in comparison with sampling fluctuations, and have been ignored in subsequent analyses.

TABLE 3

STATISTICAL TREATMENT OF COUNTS FROM TABLE 2

	Haul	Arithmetic Mean	Variance	χ_9^2	P
Copepods	I	1230.0	5020	40.814	<0.001*
	II	1460.0	Not calculated because counts were only to nearest 50		
	III	618.8	1030	13.400	0.10-0.20
Cladocera-*Penilia smackeri*	I	204.8	92.2	4.500	0.80-0.90
	II	224.8	400.3	17.808	0.02-0.05*
	III	91.8	290.0	31.593	<0.001*
Cladocera-*Evadne tergestina*	I	11.9	13.7	11.513	0.20-0.30
	II	16.5	25.9	15.635	0.05-0.10
	III	18.6	11.6	6.257	0.70-0.80
Fritillaria	I	19.8	16.7	8.455	0.30-0.50
	II	17.1	10.7	6.252	0.70-0.80
	III	2.4	2.0	8.500	0.30-0.50
Oikopleura	I	22.2	17.6	7.910	0.30-0.50
	II	24.6	16.2	6.601	0.50-0.70
	III	4.5	6.1	13.446	0.05-0.10
Chaetognaths	I	28.0	31.8	11.358	0.20-0.30
	II	32.2	34.0	10.546	0.30-0.50
	III	9.4	8.6	9.192	0.30-0.50
Fish eggs	II	1.1	0.6	5.754	0.70-0.80
	III	3.7	1.9	4.892	0.80-0.90
Fish larvae	I	1.5	1.5	9.667	0.30-0.50
	II	1.5	0.25	1.667	>0.99†
Decapod larvae	II	6.9	1.7	2.449	0.98-0.99†

* Values below the 0.95 probability level.

† Values above the 0.95 probability level.

The mean counts, variances, and χ^2 values* for the first three hauls are given in Table 3. For all other hauls, counts were made in two or four compartments only, chosen at random; the mean counts and χ^2 values are given in Table 4.

If the organisms are thoroughly mixed the counts in each set for each organism should follow a Poisson distribution. The variance should then equal the mean, and the statistic $\Sigma(x - \bar{x})^2/\bar{x}$ should be distributed as χ^2 with $(n - 1)$ degrees of freedom. The occurrence of either high or

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* $\chi^2 = \Sigma(x - \bar{x}^2)/\bar{x}$ with $(n - 1)$ degrees of freedom where x = an individual count and $\bar{x}$ = the mean of a set of 10 counts.

TABLE 4

STATISTICAL TREATMENT OF FURTHER COUNTS

	Copepods	*Penilia*	*Evadne*	Chaetognaths	*Oikopleura*	Salps	*Lucifer*	Fish Eggs	*Creseis*
Mean	400	168	46.5	25.5	6.5	8.5	14.5	3	
χ_1^2	0†	3.858	3.871	0.961	0.077	0.259	0.035	0.660	
P		0.02-0.05*	0.02-0.05*	0.70-0.80	0.70-0.80	0.50-0.70	0.80-0.90	0.30-0.50	
Mean	382	20	8	3.5	22.5	8.5			
χ_1^2	0.005	0†	0.250	0.143	0.022	1.529			
P	0.90-0.95		0.50-0.70	0.70-0.80	0.80-0.90	0.20-0.30			
Mean	420	135	53.5	6	79.5	6.5			
χ^2	4.615	3.335	0.084	1.330	0.761	0.677			
P_1	0.02-0.05*	0.05-0.10	0.70-0.80	0.20-0.30	0.30-0.50	0.30-0.50			
Mean		180	14	38.5	18				22
χ_3^2		3.120	1.500	4.441	1.150				0.975
P		0.30-0.50	0.50-0.70	0.20-0.30	0.70-0.80				0.80-0.90
Mean		226							132
χ_1^2		0.319							0.546
P		0.50-0.70							0.30-0.50
Mean	1199	342	130	34	46.5				34.5
χ_1^2	0.921	20.673	1.862	2.883	4.571				1.174
P	0.30-0.50	0.001*	0.10-0.20	0.05-0.10	0.02-0.05*				0.20-0.30
Mean	478	5		23.5	57				
χ_1^2	13.122	0†		0.192	2.246				
P	0.001*			0.50-0.70	0.10-0.20				

* Values below the 0.05 probability level.

† Values above the 0.95 probability level.

low values of χ^2 in excess of expectation may be taken as an indication that the organisms are not thoroughly mixed and therefore that the apparatus is not sampling efficiently.

In Tables 3 and 4, χ^2 values for all the organisms in any one haul are not consistently high or low. Low values are not in excess of expectation (five values altogether below the 0.95 probability level) whereas high values occur more frequently (nine values altogether above the 0.05 probability level). The high values are associated mainly with two groups of organisms, copepods and *Penilia,* particularly when they are present in large numbers. This may be explained by a strong tendency of these organisms to "clump" together when present in high concentrations.

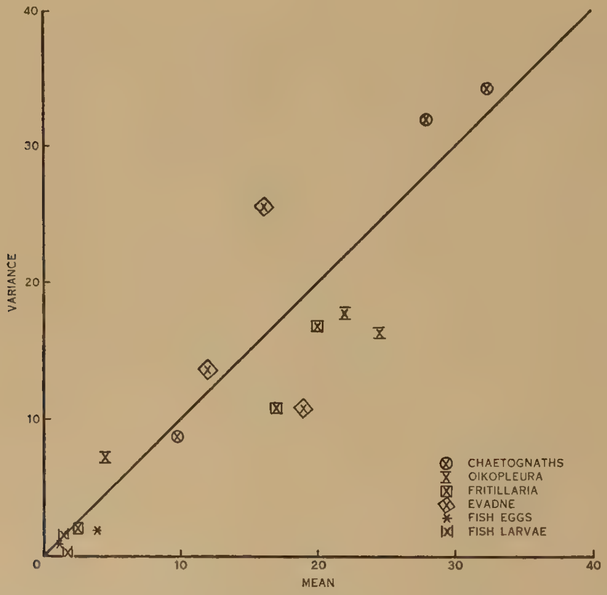
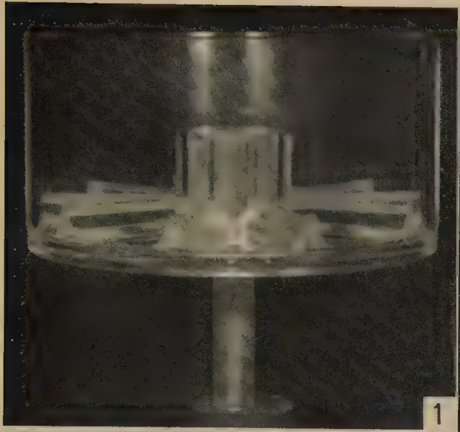


Fig. 1.—Graph showing variance plotted against the mean from Table 3 (values for *Penilia* and copepods not included).

In Figure 1, variances from Table 3 have been plotted against means for all groups except *Penilia* and copepods. The graph shows that variances and means are approximately equal, confirming the evidence already obtained from calculations of χ^2 that, for these groups, the counts do approximate to a Poisson distribution.

Despite the high χ^2 values discussed above for *Penilia* and copepods, the coefficients of variation in these cases are low and variations are well within the limits of accuracy required and achieved with the present methods of collecting plankton.

SUBSAMPLING OF PLANKTON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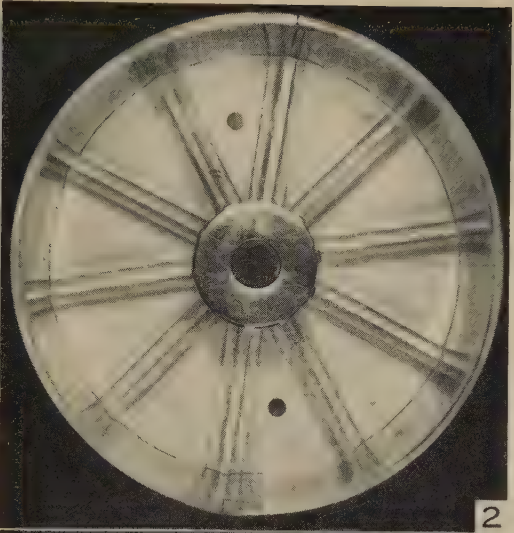
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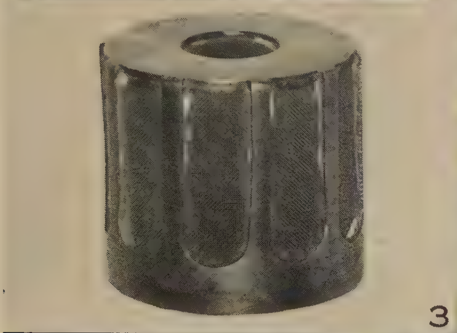
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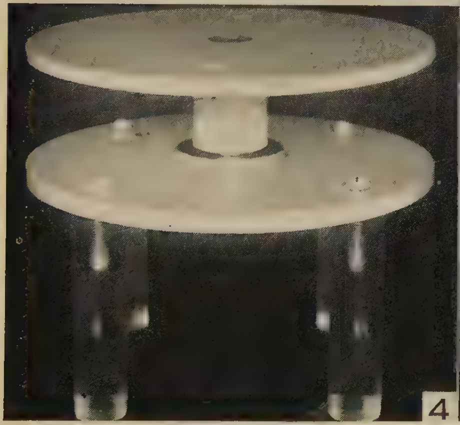
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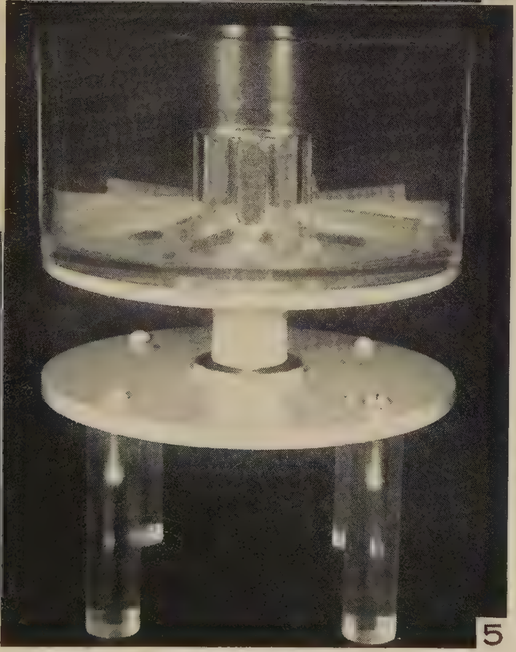
5

Fig. 1.—Vessel with the central gauze cylinder in place, lateral view.
Fig. 2.—Vessel with the central gauze cylinder in place, from above.
Fig. 3.—Central gauze cylinder.
Fig. 4.—Turntable.
Fig. 5.—Apparatus assembled.

V. ACKNOWLEDGMENTS

Thanks are due to Mr. A. Proctor for his advice and interest in the planning and during the construction of the instrument; and to Mr. George Gordon, who made the original apparatus and offered many helpful suggestions which were incorporated. For indispensable advice on the statistical treatment of the results I am especially grateful to Miss Helen Newton Turner of the Section of Mathematical Statistics, C.S.I.R.O.

VI. REFERENCE

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A CORRECTION IN THE NOMENCLATURE OF A SPECIES OF *MYCOPLANA* (EUBACTERIALES)

By E. J. F. Wood*

(*Manuscript received August* 18, 1953)

Mycoplana rosea, nom. nov.

In 1950 reference was made to *Mycoplana rubra* (Wood 1950) but although this was the first time the name was used no description was given, it being stated that the description would appear elsewhere. The description was not published until 1953 (see Wood 1953) but the name has since been found to be preoccupied by *Mycoplana rubra* (den Dooren de Jong) de Vries & Derx, this having arisen as a result of the transfer by de Vries & Derx of *Protaminobacter rubrum* den Dooren de Jong 1926 to the genus *Mycoplana* Gray & Thornton.

Hence the new name *Mycoplana rosea* is proposed for the species of Wood 1953.

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